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A REEVALUATION OF THE DERIVATION OF *QUERCUS MARGARETTA* FROM *QUERCUS GAMBELII*

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In an earlier issue of this journal a hypothesis was presented by one of us (Muller, 1952) to explain the origin of *Quercus margaretta,* an oak ranging from central and northern Texas eastward to Florida and Virginia, and *Q. drummondii,* a closely related species which occurs at the western extremity of the range of the former in central Texas. According to this hypothesis *Q. gambelii,* of the Rocky Mountain region, and *Q. stellata,* of the southeastern quarter of the United States, were the ancestral stocks from which *margaretta* and *drummondii* were derived. Stated briefly, the main points were these:

(a) During "a period of increased precipitation at the close of the Tertiary and in the Pleistocene . . . the spread of *Q. Gambelii* stock eastward over the southern plains area would have been possible. Simultaneously, the westward extension of *Q. stellata* from an eastern center could have occurred. The two prototypes would have met either on the plains or to the east of that area" (*op. cit.:* 158).

(b) The ancestral *Q. gambelii* stock migrated along the Gulf Coastal Plain eastward to the Atlantic.

(c) ". . . dessication of the entire region has resulted in recession of the prototypes from the southern Great Plains and consequent isolation of the Gulf Coast populations from those of the Rocky Mountains" (*op. cit.:* 158).

(d) The western end of the Gulf Coast population, through introgression from *Q. stellata,* has been modified to form the population known as *Q. drummondii.* "The lesser gene flow in the east has left the *Q. Gambelii* stock relatively unchanged so that the speciation of this population (as *Q. Margaretta*) has in large part resulted from its isolation from the ancestral *Q. Gambelii* and only slightly from hybridization with *Q. stellata*" (*op. cit.:* 159).

Current studies (by Tucker) of *Quercus undulata,* a hybrid complex centered in the Rocky Mountain region and undoubtedly involving *Q. gambelii* as one parent, have inspired great interest in the extent and time of past migrations of *Q. gambelii* stock. Continued study (by Muller) of the relations amongst *Q. stellata, Q. margaretta,* and *Q. drummondii* similarly retain the origins of these species as foci of interest. The question of

participation of *Q. gambelii* in any of these origins thus remains open. Having pondered at length the details of the above hypothesis, and having examined a number of fields that might be expected to provide evidence bearing on the matter, we have concurred in a quite contrary conclusion.

It is our considered judgment that *Quercus gambelii* did not make any *extensive* eastward migration as recently as Pleistocene or late Pliocene, and that *Q. margaretta,* whatever its ancestry may have been, has not been of such recent derivation. Rather, such similarities as these species show to one another are probably best interpreted as characters indicative of an ancient common ancestry, not more recent than Middle Tertiary (at most, Late Miocene).

It is the purpose of the following critique, therefore, (1) to consider the hypothesis in more detail, (2) present evidence which in our opinion renders it untenable, and (3) to offer suggestions to account for some, at least, of the principal phenomena involved.

Morphological Relationships Between *Quercus gambelii* and *Q. margaretta*

The assumption of a close relationship between *Quercus gambelii* and *Q. margaretta* is based largely on presumed morphological similarity: ". . . the fundamental characters of *Q. margaretta* reveal a close relationship to *Q. gambelii.* The latter species shares with *Q. margaretta* its glabrous brown twigs, red buds, persistent stipules, round-lobed leaves with usually narrow sinuses, glossy upper leaf surfaces, loosely spreading pubescence of the lower leaf surface, and short-peduncled fruit" (*op. cit.:* 159).

Let us examine these points one by one, and consider not only these presumed similarities, but the differences between the two species, as well.

Twigs. There are, it is true, some points of similarity in twig characters, but none that is at all constant. Besides, the characters in which they are sometimes similar show different patterns of variation in the two species. Furthermore, the points of difference are certainly as numerous as the points of similarity.

In *Quercus margaretta* the mature twigs of the current season are most commonly rather light grayish-brown, varying to gray or light brown, or to dark grayish-brown. In *Q. gambelii* they are quite frequently light grayish-brown, also, but may be light or medium brown, and particularly reddish-brown. In the following several seasons, the branchlets assume a medium to dark gray color in *Q. margaretta.* The same shades are to be seen in *Q. gambelii* also, but in the latter not infrequently the older branchlets are a pale ashy gray, at times nearly white.

In *Q. margaretta* twigs of the current season are usually quite glabrous, or only infrequently glabrate (glabrous except for a few, scattered, persistent hairs). In *Q. gambelii,* however, they are most commonly sparsely to moderately puberulent (infrequently densely so), varying to glabrate, or infrequently, being quite glabrous.

A further difference is seen in the common tendency shown by *Q. gcmbelii* for small transverse fissures to develop in the periderm layer of twigs of the current season. These are usually quite apparent to the unaided eye, once they are well-developed, and seem to be present most abundantly on the longer, more vigorous twigs. A large majority of the specimens examined in this study show such fissures. In *Q. margaretta,* on the other hand, they are rarely encountered—we have observed them in only 2 out of 69 specimens examined.

Buds. Bud color is actually distinctly different in the two species, rather than constituting a point of close similarity. In *Q. margaretta* the buds are characteristically a dark reddish-brown (commonly approximating "piccadilly," plate 7, 10-H, in Maerz and Paul, 1930), while in *Q. gambelii* they are a lighter shade,

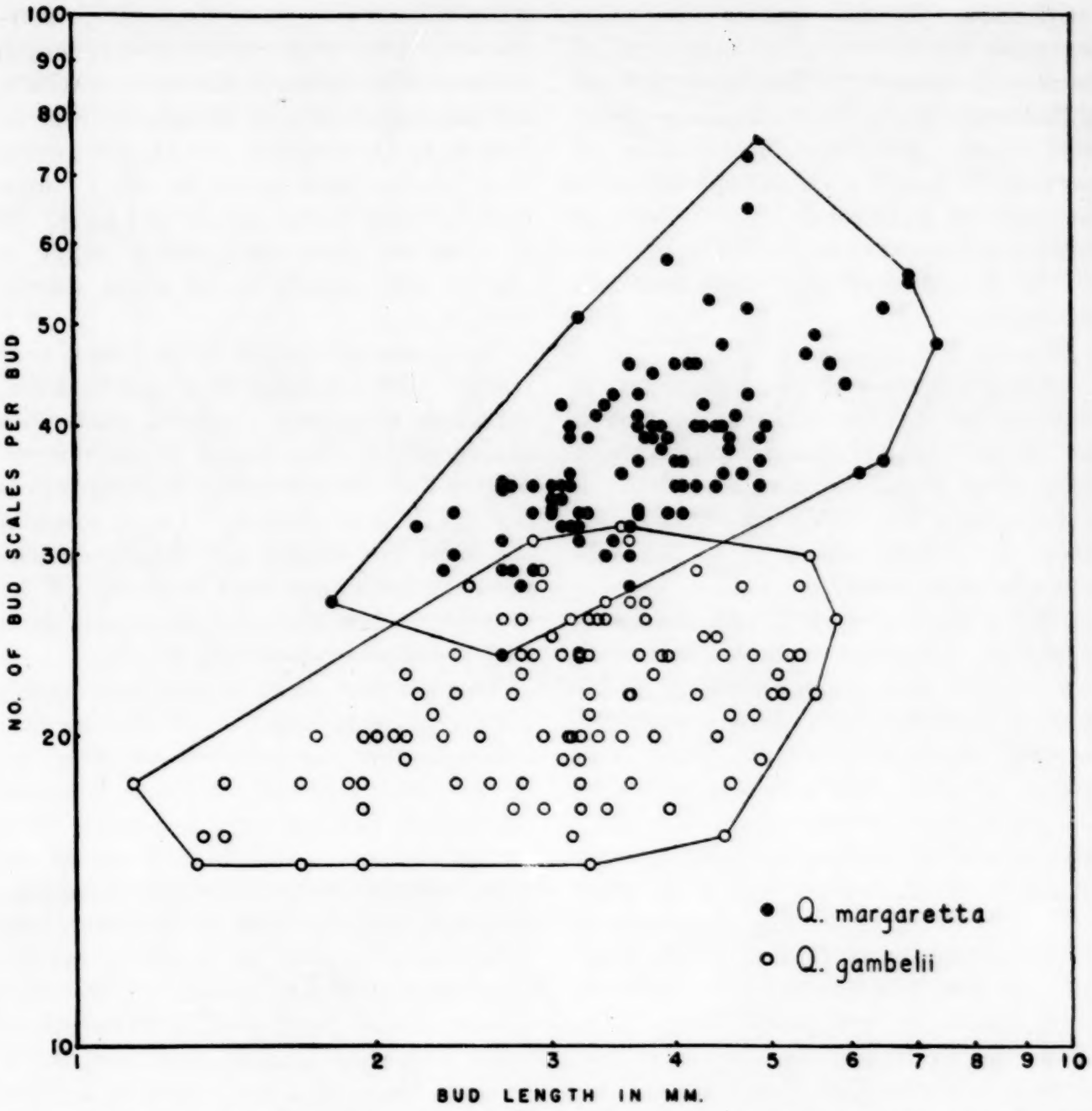

FIG. 1. Scatter diagram showing the correlation between bud size and number of bud scales per bud in *Quercus margaretta* and *Q. gambelii*. Each symbol represents one bud. (See appendix for list of specimens included in this analysis.)

and usually an orange-brown (approximating one of the shades from "rust" to "tarragona," plate 6, 12-A to -G, *op. cit.*). After examining and comparing a sizeable series of specimens of the two species, one comes to recognize readily this distinctive and quite consistent difference. Exceptions are to be found only infrequently, the lightest colored buds of *Q. margaretta* approaching the darkest of *Q. gambelii*.

Another difference is to be noted in the number of bud scales per bud. In buds of comparable size, *Q. margaretta* commonly has a higher number than *Q. gambelii* (fig. 1). Moreover, the two species seem to show a difference in the morphogenetic pattern of bud development. The number of bud scales seems in general to increase at a greater rate (with increasing bud size) in *Q. margaretta* than in *Q. gambelii*.

In the process of checking these points, twenty specimens of each species were examined. Bud scales were counted down to the first recognizable young foliage leaf, and counts were obtained for five buds from each specimen.

Stipules. The two species do show a degree of persistence of at least some of the stipules around the bud(s) at the end of the branchlets. They seem to be somewhat more consistently persistent in *Q. gambelii,* however. Of 60 specimens of this species examined, only 5 had no stipules persistent at all, while in *Q. margaretta* 19 out of 60 specimens had none persistent.

Leaves.

Round lobes—This is a character so common among the white oaks that it can scarcely be taken as an indication of really close phylogenetic relationship. It is shared by a large majority of the deciduous lobed-leaved members of the subgenus *Lepidobalanus.*

Narrow sinuses—Quercus gambelii most commonly does have narrow sinuses, it is true. So, also, may occasional specimens of *Q. margaretta.* Most commonly, however, the *whole pattern of leaf form* is quite different in the two species (fig. 2). As Muller intimates (*op. cit.:* 159), leaf form in *Q. margaretta* is often more suggestive of *Q. stellata* than of *Q. gambelii.* But even considering specimens of *Q. margaretta* most similar to *Q. gambelii,* the two characteristically differ in other details of leaf morphology. The latter usually has more lobes per leaf, which are relatively narrower than in *Q. margaretta,* and also usually has relatively longer petioles.

Glossy upper leaf surfaces—This is undoubtedly a point of similarity, but, like rounded lobes, it is a character shared by many other white oak species, and is scarcely a useful criterion of really close relationship.

Pubescence of the lower leaf surface—Any gross similarities that may be apparent in the pubescence of the lower leaf surface on casual inspection are far outweighed by the striking differences readily apparent on closer examination. In both species the pubescence consists in large part of stellate hairs, although in younger leaves, before any of the pubescence becomes detached, it usually appears thicker and more dense in *Q. margaretta.* This is due to the greater length of the stellate hairs of this species, which, not uncommonly, may be almost twice as long as in *Q. gambelii.* In *Q. margaretta* their approximate range is .47–.72 mm, usually being about .50–.55 mm long. In *Q. gambelii* their approximate range is .20–.40 mm, usually being about .24–.32 mm long.

In *Q. margaretta* the hairs detach very readily, each breaking off at the base and detaching as a unit. Indeed, so readily deciduous are they that it is not uncommon to find sizeable areas on older leaves that are largely glabrate. In *Q. gambelii* the hairs are usually not readily detachable, the individual rays breaking off irregularly when one tries to detach them with a scalpel or dissecting needle.

The number of rays per hair varies within different limits in the two species, although their ray numbers overlap. In *Q. gambelii* perhaps the most frequent ray number is 4, although 2–3-rayed hairs are very common, and in some specimens even simple hairs may predominate. Numbers higher than 4, however, are rather rare (in pure *Q. gambelii,* not introgressed by any of several small-leaved species of the Southwest, with which it may hybridize). In *Q. margaretta* 4-rayed hairs are not uncommon, but higher numbers are more frequent, numbers as high as 8 being common.

Perhaps the most distinctive differences of the stellate hairs are the following: in *Q. margaretta* the basal portion of the rays are fused to form a short, erect, trunk-like portion which is inserted on a small rounded knob-like protuberance. In *Q. gambelii* the rays are not fused, being free virtually to the base; and the hairs are not borne on protuberances (fig. 3). These differences are of an order one ordinarily sees only between species widely separated taxonomically, and in this case would seem to indicate a long period of separate evolutionary divergence for the two.

The stomata provide still another dif-

ference which, however, is not as distinctive or constant as are the trichome differences. In *Q. margaretta* they are often whitish and stand out quite conspicuously against the ground color of the surrounding cells of the lower epidermis when seen in surface view with reflected light, at ca. 100 ×. There is probably a

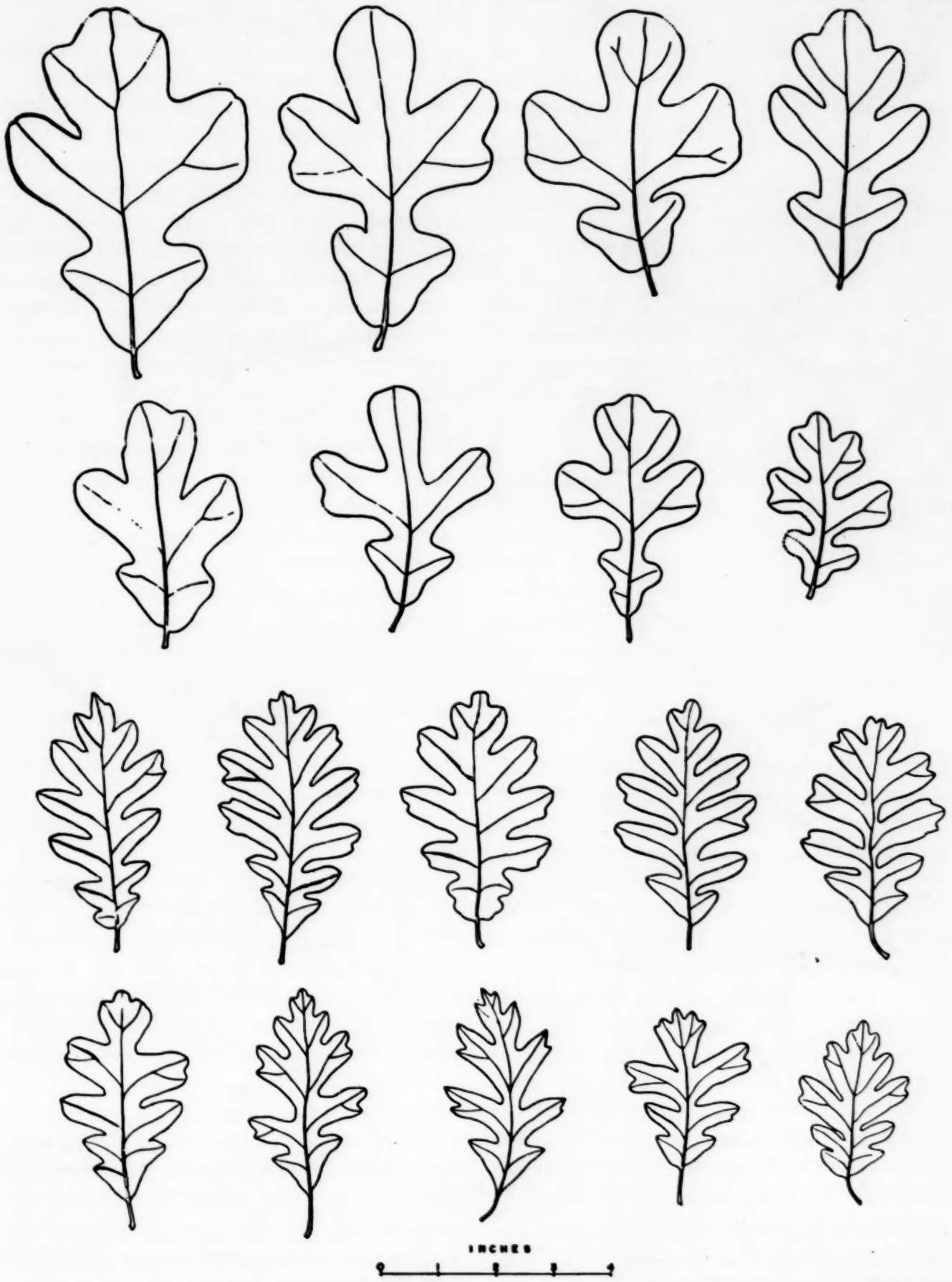

FIG. 2. Tracings of representative leaves from specimens of *Quercus margaretta* (two upper rows) and *Q. gambelii* (two lower rows). (See appendix for list of specimens.)

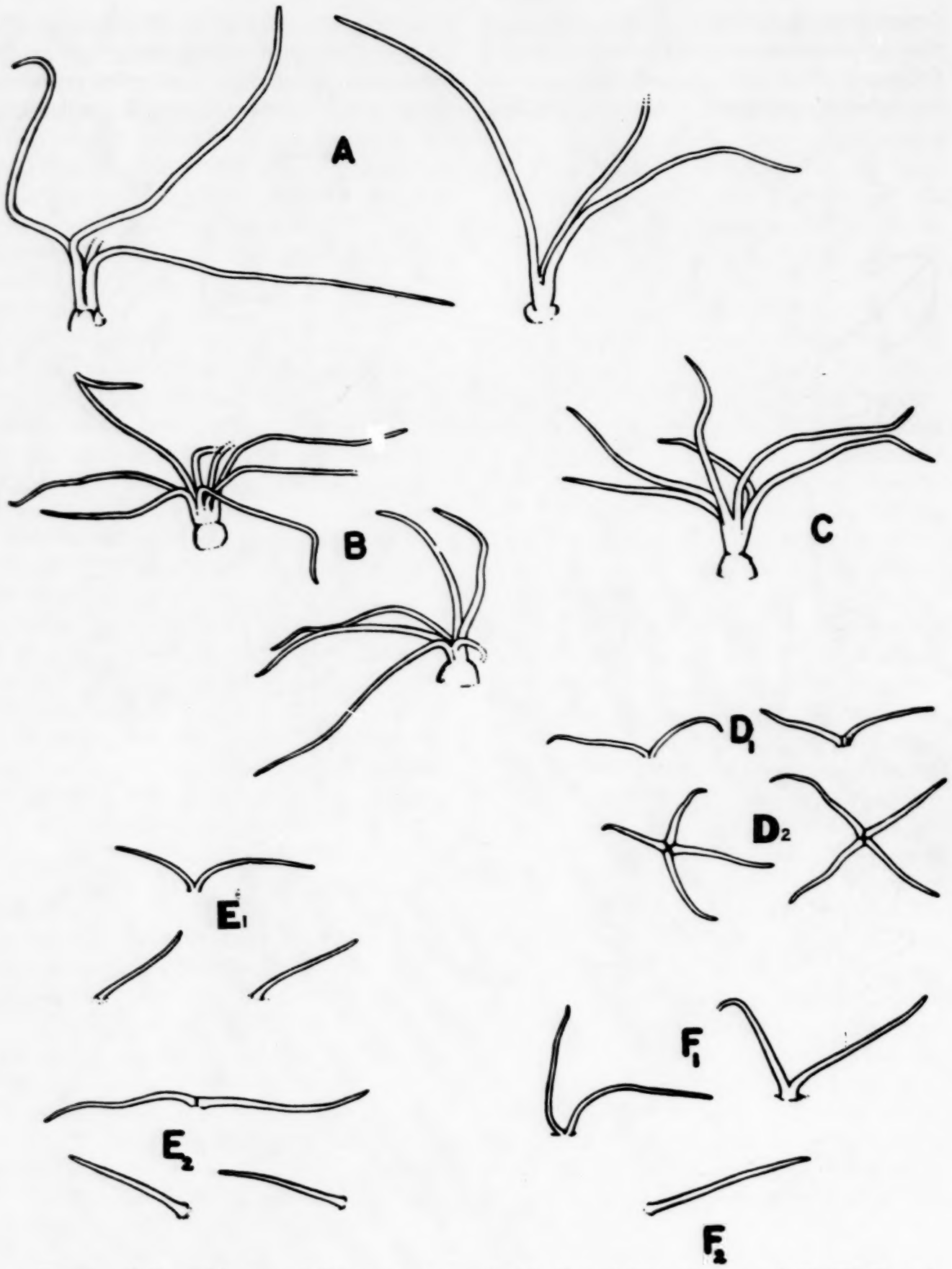

FIG. 3. Foliar trichomes of *Quercus margaretta* (A, B, and C) and *Q. gambelii* (D, E, and F). (A, B, C, D_1, E_1, and F_1: seen from the side; D_2, E_2 and F_2: seen from above. All drawn to the same scale.) (See appendix for list of specimens.)

correlation between this distinctive appearance and the fact that the guard cells are somewhat elevated above the surface of the epidermis. In *Q. gambelii,* on the other hand, the stomata are usually the same color as the surrounding epidermal cells and are quite inconspicuous; so much so, in fact, that at times they are

discernible only after careful focussing and close scrutiny. The guard cells, as seen in section view, are slightly, or not at all, elevated above the surrounding epidermal cells.

Among the specimens of *Q. margaretta* examined, even those most similar to *Q. gambelii* in leaf form alone (e.g., C. H. Muller 8745, S.M.U.; fig. 2, second row, right end) show clearly, nevertheless, the microscopic details of typical *Q. margaretta*—the large stellate hairs with rays fused at the base, the small rounded pedestal-like protuberances on which they are borne, and the conspicuous, whitish stomata. On these details alone such specimens can be distinguished from *Q. gambelii* without the slightest hesitation.

The details of epidermal structure here described for *Q. margaretta* are abundantly developed in many of the white oak species of Mexico. For instance, *Q. centralis,* which is widespread in the Cordilleran region, has both prominent white stomata and detachable stellate trichomes with fused bases (lacking, however, the pedestal attachment). The prominent stomata, furthermore, are characteristic of several white oaks of the eastern United States, notably *Q. alba* and *Q. chapmani.* The lack of prominent white stomata, a character shared by *Q. gambelii,* and *Q. garryana* of the Northwest, seems to be much less widespread in the subgenus.

Short-peduncled fruit—This is a point of similarity, to be sure, but one which is shared by so many other species of the subgenus *Lepidobalanus* that it can scarcely be taken as an indication of really close phylogenetic relationship. On the other hand, the acorn cup scales show some rather distinct differences. In *Q. margaretta* they are only slightly thickened basally, and have narrow elongated tips which are often rather loosely appressed. In *Q. gambelii* the cup scales are commonly much more prominently thickened basally, with shorter, usually closely appressed tips.

From the foregoing discussion it will be apparent that (1) several of the points of similarity cited by Muller are actually characters common to many other white oaks, (2) the differences between *Q. margaretta* and *Q. gambelii* are more numerous than the actual similarities, and (3) the most distinctive of these differences are of an order one commonly encounters between species that are widely separated taxonomically. These differences argue against a really close phylogenetic relationship.

Biotic Associates of *Quercus gambelii*

A second line of evidence is furnished by biotic associates of *Quercus gambelii.* Any climatic change permitting the latter to migrate might be expected to permit a similar migration on the part of associated species having very similar ranges of tolerance for climatic factors. Thus, if this oak had made the migration postulated, it would be quite in line with expectation to find at least some of its Rocky Mountain associates, or closely related derivative forms, in the general range of *Q. margaretta* today. That this is hardly the case in those plant and animal groups of the Rockies exhibiting the closest association with *Q. gambelii* will now be shown.

The Oak Gall Wasp Genus, *Cynips*

All members of the genus *Cynips* (as delimited by A. C. Kinsey) are restricted to oaks (i.e., they are obligate parasites) of the two subgenera, *Lepidobalanus* (*Leucobalanus* of Trelease, 1924), the White Oaks, and *Protobalanus,* the Intermediate Oaks (Kinsey, 1930: 47). The species with which we are concerned are, of course, white oaks.

It should be pointed out, for the benefit of those who may be unfamilair with Kinsey's published works, that the terminology applied to the lower taxonomic units differs in the two major papers cited in the following discussion (1930, 1936). In his extensive monograph of 1930 the primary unit is the variety, and a group of closely related varieties is a species. In his 1936 paper, however, the primary unit is designated a species, and aggrega-

tions of such units are designated complexes. Thus, the "variety" of his 1930 monograph is the "species" of his 1936 paper, and his "species" of 1930 becomes the "complex" of his 1936 paper. In the following discussion, his terminology of 1936 is used.

The extent to which any complex or species of *Cynips* is restricted to any particular species of oak evidently varies widely (cf. Kinsey, 1936: 323–328). A few species complexes are quite specific in their host requirements, occurring over a broad geographic area on only one or two species of oak (for example, all four species of the *C. centricola* complex are restricted to *Q. stellata*). At the other extreme are cases such as the *C. bella* complex (comprising five species), a single species of which (*C. bella* Bassett) is recorded from *Q. grisea, Q. undulata, Q. chihuahuensis, Q. oblongifolia, Q. arizonica* (incl. *Q. sacame* Trel.), *Q. reticulata* (*Q. diversicolor* Trel.), *Q. gambelii,* and *Q. toumeyi* (1936: 173).

In what way, then, can data from these gall wasps help to solve our problem? If *Quercus gambelii* had made the postulated migration, it would seem logical to expect that at least a few of the 12 *Cynips* species recorded from it (1936: 323–328) might have migrated along with their host species, resulting in a close similarity between the *Cynips* species of *Q. gambelii* and *Q. margaretta* today. The evidence bearing on this matter may be summarized as follows:

1. None of the several species complexes of *Cynips* that occur on *Quercus gambelii* (*Q. gambelii, Q. submollis, Q. utahensis*) *and on eastern oaks as well,* has representatives on *Q. margaretta* or (save for one minor exception in the *C. fulvicollis* complex, discussed below) on *Q. stellata.* The species on *Q. gambelii* have their closest eastern relatives on *Q. macrocarpa,* or, in one case, on *Q. alba.*

2. Conversely, the species complexes that *do* occur on *Q. stellata* and its very close relatives, including *Q. margaretta,* are not known to occur on *Q. gambelii* at all.

A discussion of these points in greater detail will be profitable. First of all, the species complexes that occur on *Q. gambelii* and also on eastern oaks are the *Cynips fulvicollis, villosa, pezomachoides,* and *hirta* complexes.

In the *C. fulvicollis* complex two closely related species are known from *Q. gambelii—C. latigenae* in Utah, and *C. insulensis.* The latter, in addition to occurring on *Q. gambelii* in the Colorado Rockies, occurs on *Q. macrocarpa* in the Black Hills, and on the same host from the eastern part of the Dakotas across Minnesota and Wisconsin. In addition to *Q. macrocarpa,* several other eastern oaks serve as host to members of this complex: *Q. alba, Q. bicolor, Q. lyrata, Q. muhlenbergii,* and *Q. prinus* (*Q. michauxii*). *C. rubricosa,* an apparently rather rare species of the complex, is recorded on *Q. stellata* from a single collection from Marshall, Texas (*Q. alba* being a more common host). It was Kinsey's opinion that the evidence clearly indicates "that the *fulvicollis* complex was of Rocky Mountain origin, first inhabiting *Quercus gambelii* and *Q. macrocarpa,* and that its abundance on *Q. alba* in the east is the derived condition and of more recent date" (1936: 207).

In the *C. villosa* complex there are also two closely related species known from *Q. gambelii: C. calvescens* in Utah and *C. alaria* in Colorado and northern New Mexico. They have a common close relative (1930: 355) in *C. villosa* occurring on *Q. macrocarpa* in the Black Hills of South Dakota, the northeastern corner of Wyoming (1936: 263), and in the more northern Middle West, from northeastern Kansas extending eastward into New York state.

In the *C. pezomachoides* complex one species, *C. cincturata,* is known from *Q. gambelii* in Colorado. The other eight species of the complex are known only from *Q. alba* of the Middle West and eastern states. Kinsey expressed the view that "The Rocky Mountain material of the species [complex] testifies to the origin of the group at a period before the

Great Plains became so arid as to exterminate the oak forests that once connected the Southwestern and more Eastern relatives" (1930: 374).

Finally, in the *C. hirta* complex five species are known from *Q. gambelii* in Utah, northern Arizona, Colorado, and New Mexico. The most easterly of these, *C. undulata* (occurring on *Q. gambelii*—*not Q. undulata*), is the only one of these five occurring east of the continental divide; it occurs in northern New Mexico and Colorado. Kinsey's observations regarding its affinities are interesting: "The Eastern Colorado species (*undulata*) is, it is surprising to find, more closely related to the *scelesta-opima-macrescens* group of the eastern quarter of the United States [all of which occur on *Q. macrocarpa*]. This is additional evidence of the Rocky Mountain origin of a portion of our Eastern American insect fauna. The Black Hills material, geographically and geologically closer to the Rocky Mountain area, is not too certainly determinable, but it appears to represent the Eastern species *macrescens*" (1936: 281).

Now, as to the species complexes occurring on *Quercus stellata, Q. margaretta,* and their close relatives, we find there are two—the *C. centricola* and *C. mellea* complexes. As stated previously, neither has representatives on *Q. gambelii.* If one had consulted only Kinsey's 1930 work, however, the inference might well be drawn that the *centricola* complex was very closely related to, and probably derived from, the *dugesi* or *bella* complexes of the Rocky Mountains (cf. p. 71) —both of which *do* have representatives on *Q. gambelii.* It should be noted, however, that Kinsey's later (1936) opinions regarding the origin of the *centricola* complex are quite different: ". . . the Eastern American complex, *centricola,* remains unconnected. Failing to find *centricola* in the Eastern Sierra of Mexico, we are at a loss to know where to look for the origin of the group" (p. 79). His feeling, nevertheless, was that it was not from the *bella* or *dugesi* complexes in the Rocky Mountains of the U. S. (oral communication, 1956: also cf. fig. 10, 1936). Although he indicated that the Texas and Gulf Coast members of the *centricola* complex are still imperfectly known (p. 180), present indications are that this complex is restricted to *Q. stellata.*

The *C. mellea* complex is known, for the most part, from *Q. stellata, Q. margaretta,* and closely related oaks. Several members of the complex are known from other oaks (e.g., *Q. alba*), but for the most part, they are quite a different group of oaks from those frequented by the four *Cynips* complexes on *Q. gambelii* discussed above (the *fulvicollis, villosa, pezomachoides,* and *hirta* complexes). One species of the *C. mellea* complex, *C. rydbergiana,* occurs in the Rocky Mountain area on oaks of the *Quercus undulata* alliance, which *is* related to *Q. gambelii.* Nevertheless, *C. rydbergiana* is not recorded from the latter oak, itself.

Among the total of 12 species of *Cynips* listed as occurring on *Quercus gambelii* (1936: 323–328), one would expect to find at least a few very closely related (if not identical) species on *Q. margaretta,* if Muller's hypothesis were valid. The data presented above, however, indicate clearly that this is not the case; indeed, not even the same species *complexes* are common to the two oaks.

These facts present a serious challenge to the hypothesis that *Q. gambelii* gave rise to *Q. margaretta* by means of a geologically recent eastward migration. They must, however, be examined with some care lest the distribution of *Cynips* assume more than its rightful significance in problems of the history of *Quercus* species.

The degree of completeness with which *Cynips* has been collected does not approach that of *Quercus* in spite of the numerous collections made by Kinsey. It must be remembered that his collections were mass collections of galls from which he reared the adult stages of the parasites. Thus, he often took a hundred specimens from one tree and his thousands of specimens thus represent few host individuals. The oaks, on the other hand, are repre-

sented by literally thousands of collection sites constituting a far more full coverage of the geographic area involved.

Of more serious significance is the fact that the insect is dependent upon the tree and not the tree upon the insect. It is therefore not a foregone conclusion that a parasite migrating with a tree could survive temperature or other ecological changes to which a long migration might subject it and which the host might weather successfully. We obviously have no way of knowing what species complexes of *Cynips* might have inhabited *Q. margaretta* during Late Tertiary time.

It must also be emphasized that Kinsey espoused a series of postulates (1936: 24–25) of a highly controversial nature. He states, for instance, that "Closely related species may, as a result of major mutation, be very dissimilar" and "Where the morphologic and distributional data are contradictory, the distributional data may assume prime significance." With these points prominent in his thinking, it is difficult to see how Kinsey could have recognized a wide disjunction had he encountered one.

We must emphasize the value of positive evidence derived from similarity of parasite faunas in indicating possible relationships of two host populations (although the facultative distribution of some *Cynips* complexes on totally unrelated *Quercus* species would tend to throw some doubt on even this—for instance, *Q. gambelii* and *Q. alba* are very remotely related in spite of their being common hosts to two different *Cynips* complexes. Negative evidence, on the other hand, unless it is correlated (as in the present instance) with negative morphological evidence in the oaks themselves, is of even more questionable significance.

Birds and Mammals of the Ponderosa Pine Zone

A number of birds and mammals of the ponderosa pine zone are known to be partially dependent on acorns as a source of food. Since *Quercus gambelii* is the only oak in most such areas in the Rockies, this, of course, implies a dependence of some degree on *Q. gambelii.* Probably the best-established cases of Rocky Mountain birds known to feed on acorns would include the jays, the wild turkey, certain woodpeckers, and the band-tailed pigeon. The mammals most certainly known to be balanophagous are squirrels, chipmunks, the black bear, and, to a lesser extent, wood rats. Since these birds and mammals are, in some degree, dependent on *Q. gambelii,* as a source of food, and since their ranges of tolerance for climatic factors at least partially overlap those of the oak, it would seem logical that a climatic change which would permit *Q. gambelii* to migrate would have permited similar migrations by some, at least, of its bird and mammal associates. The relationships between such species of the Rocky Mountain ponderosa pine zone and their counterparts in the range of *Q. margaretta,* therefore, would seem to be especially pertinent to our problem.

Of the jays in the Rocky Mountain region, undoubtedly the characteristic species of the ponderosa pine forest is the Steller's jay, *Cyanocitta stelleri diademata.* It is known, furthermore, to feed abundantly on acorns in the fall and winter months (Bent, 1946). Another species, Woodhouse's jay, *Aphelocoma coerulescens woodhouseii,* is common in the pinyon-juniper woodland of lower elevations, but it may ascend into associations where *Quercus gambelii* occurs (Pitelka, 1951: 288). In such areas acorns probably form a substantial part of its diet in the fall (Bent, *op. cit.*).

As to the counterparts of these jays in the Gulf Coast, or the southeast in general, it may be noted that *Cyanocitta stelleri* is entirely restricted to the western states, having no eastern races at all. Its nearest relative in the east is the eastern blue jay, *C. cristata,* which, of course, is a different species. *Aphelocoma coerulescens,* on the other hand, does have an eastern race (*A. c. coerulescens*) in peninsular Florida, although the species is not

represented in the region between Florida and the Edwards Plateau of west-central Texas. Woodhouse's jay, however, has its closest affinities with races occurring to the south of its range, in Mexico, rather than with the Florida race. The isolation of the latter from the remainder of the species, moreover, probably antedates the Pleistocene, and may date from early Pliocene (cf. Pitelka, 1951: 373, 382–383).

It seems to be a matter of common knowledge that the wild turkey, *Meleagris gallopavo,* eats acorns freely during the fall and winter months. Indeed, according to Leopold (1944: 155), it prefers them to other items of diet. This species, which comprises five geographic races, was originally distributed from Arizona to the eastern seaboard (cf. Trippensee, 1948, map: 305), thus spanning the range of both *Q. gambelii* and *Q. margaretta.* The wild turkeys of the southern Rocky Mountain region constitute a different race, *M. g. merriami,* from those of the eastern states and the gulf coast (exclusive of peninsular Florida), *M. g. silvestris,* although distinguishing differences are quite slight. Within the species as a whole, however, there seems to be little if any pattern of specialization that would suggest which segment, if any, might be considered ancestral, and from which inferences might be drawn regarding direction of subsequent migrations. Furthermore, there is little, if any, pattern in the known fossil record of the species that would shed light on this problem (Hildegarde Howard, written communication, Jan. 29, 1957). Thus, although it is possible that the spread of the species from an ancestral center of dispersal may have followed, in general, a migration pattern similar in time and direction to that postulated for *Q. gambelii,* evidence in support of this has yet to be discovered.

Of the woodpeckers known to occur regularly in the ponderosa pine zone of the Rockies (Bent, 1939), acorns constitute a sizeable proportion of the diet apparently in only the following two species: the Lewis woodpecker, *Asyndesmus lewisi* (Beal, 1911), and the acorn woodpecker, *Balanosphyra formicivora aculeata* (Bent, 1939: 225). Both of these species are members of western genera, which have no representatives at all in the central or eastern parts of the country. A few other species are known to eat acorns on occasion (e.g., Rocky Mountain races of *Colaptes cafer* and *Dryobates villosus*), but evidently such fare constitutes only a minor proportion of their total diet (Beal, *op. cit.*).

The band-tailed pigeon, *Columba fasciata fasciata,* ranges widely over western North America including the Rocky Mountain region. In the fall and winter the chief food of this species, apparently, is acorns (Bent, 1932). It does not range east of the mountains of West Texas, however, nor are there any closely related species in the eastern states.

Of the tree squirrels, the tassel-eared squirrel, *Sciurus aberti,* is the only one at all closely associated with the ponderosa pine zone in the Rocky Mountain region. That this species eats and stores acorns seems well-established (Bailey, 1931: 70), although in general it is much more closely dependent on ponderosa pine for food. It has no really close relatives among the tree squirrels of the eastern states, and even the closest (the eastern gray squirrel, *Sciurus carolinensis,* and eastern fox squirrel, *S. niger*) are considered to be subgenerically distinct from it (Howell, 1938).

Certain ground squirrels that may occur in the ponderosa pine zone (e.g., *Citellus variegatus*) apparently are known to eat and store acorns (Howell, 1938: 23). The species that enter this zone, however, are evidently all western in their distributions, and are treated as being subgenerically distinct from the few species (of the Great Plains) that range farther to the east (*op. cit.*). Indeed, in the southeastern quarter of the country ground squirrels seem to be nearly or quite lacking.

Chipmunks (*Tamias* and *Eutamias*)

are known to eat, transport, and store acorns (cf. Howell, 1929: 9–10). The species of the Rocky Mountains and the western states generally, however, are apparently not closely related to the eastern chipmunks. Indeed, the two groups are usually considered to be generically distinct (Howell, 1929; White, 1953).

The black bear, *Ursus americanus,* eats acorns freely (Trippensee, 1948: 172). "Originally [it] could be found throughout the wooded sections of North America" (*op. cit.:* 169), and thus occupied at least p[illegible]tions of the ranges of both our oak species. According to Erdbrink, "this bear has occurred in North America probably since the lower Pleistocene" (1953: 310). There seems to be little if any ground, however, either from any pattern of intraspecific specialization or from the fossil record (Hay, 1923, 1924; Erdbrink, *op. cit.*), on which to base opinions of time or direction of migrations. Thus, as in the case of the wild turkey, it is possible that the black bear may have undergone a migration similar to that postulated for *Q. gambelii,* but as yet we have no evidence of this.

Wood rats (*Neotoma* spp.) also probably eat acorns on occasion (cf. Goldman, 1910: 11). The most common ponderosa pine zone species of the central and southern Rockies generally is *Neotoma mexicana,* although *N. albigula,* of the Sonoran Zones and *N. cinerea,* of the Boreal Zones, may also be found sparingly in the lower and upper levels, respectively, of the ponderosa pine zone (J. S. Findley, oral communication). These species, however, are apparently not very closely related to the wood rats of the southern states. Goldman (1910) places these three in different species groups from the one species, *N. floridana,* of central Texas and the Gulf Coast. *N. cinerea,* in fact, is subgenerically distinct from *N. floridana.*

Associated Plant Species

For purposes of comparison, and before checking any manuals of the southern flora, a list of ten of the most commonly observed woody plant associates of *Quercus gambelii* over most of its range was compiled. This included *Pinus ponderosa, Pinus edulis, Pseudotsuga taxifolia, Juniperus scopulorum, Populus tremuloides, Cercocarpus montanus, Amelanchier* spp. (*A. alnifolia* or closely related forms), *Prunus virginiana* var. *melanocarpa, Robinia neomexicana,* and *Ceanothus fendleri.* Certain of these (e.g., *Pinus ponderosa* and *Juniperus scopulorum*) are more consistent associates of *Q. gambelii* than others; some are associated with it mainly toward its upper altitudinal limits (e.g., *Pseudotsuga taxifolia* and *Populus tremuloides*), others toward its lower limits (e.g., *Pinus edulis*), etc. Still, they all have ecological requirements that at least partially overlap those of *Q. gambelii,* and it might logically be assumed that a climatic shift that would permit the latter to migrate would also permit at least some of the others to do so.

A check, first of all, of the flora of Texas as a whole (Cory and Parks, 1937) and the southeastern states (Small, 1933) gives the following results. In Texas the majority of these ten associates of *Q. gambelii* are known from the trans-Pecos portion of the state. This is entirely in line with expectation, of course, for the upper slopes of the higher mountains harbor small areas of ponderosa pine zone vegetation (including *Q. gambelii,* itself). *Pinus edulis,* in addition, extends eastward onto the Edwards Plateau. None of these, however, (except *Prunus virginiana*—but *not* the var. *melanocarpa*), is recorded from east of the Edwards Plateau. Similarly, for the southeastern states generally, the only species of the list recorded (Small, 1933) are *Prunus virginiana* (but not the var. *melanocarpa*) and *Populus tremuloides.* The former is extremely widespread in the eastern half of the continent and there would seem to be little doubt that its existence there extends back before Pleistocene time. The latter is recorded for the

mountainous regions of Tennessee only, where its occurrence clearly represents the southeastern extremity of a more or less continuous boreal distribution which is transcontinental farther northward (cf. map p. 157, Collingwood and Brush, 1947).

Reference to floras of more local scope corroborates the above observations. Thus, none of the ten (except, again, *Prunus virginiana*) is recorded for south-central or eastern Texas (Young, 1920; Reeves and Bain, 1947; Tharp, 1926), nor from the Gulf Coastal Plain farther eastward (Mohr, 1901; Thorne, 1954). Furthermore, a comparison of floristic associations of these areas (Mohr, *op. cit.:* 94–118; Tharp, *op. cit.:* 32–34, 41–45, 50–54) with associations characteristic of the ponderosa pine zone of the central and southern Rockies (Standley, 1915: 187–191; Shreve, 1942: 20–22; Costello, 1954: vi–viii) merely serves to underscore the striking floristic differences between the two areas.

If *Q. gambelii* succeeded in reaching the favorable rainfall belts of Central Texas, it would seem that others amongst its common associates should have done likewise. The lack of any clear evidence that its principal plant associates, the more important balanophagous animal associates, or its Cynipid parasites made such an eastward migration would cast considerable doubt on the postulated recent migration of *Q. gambelii.* Their absence (except for the wild turkey and black bear) from the range of *Q. margaretta* suggests that if the two oak species had a common origin, it was sufficiently remote in geologic time to have allowed elimination of virtually all close common associates.

Edaphic Preferences of *Quercus gambelii* and *Q. margaretta*

Additional evidence bearing on the relationship between these oaks was sought in a comparison of their edaphic preferences. The requirements of *Q. margaretta* are indicated as follows: "The distribution of *Q. margaretta* is determined by the extent within its general range of beds of deep sand, of which it is an obligate inhabitant" (Muller, *op. cit.:* 153). Then, in outlining the manner in which *Q. gambelii* could have migrated eastward to come in contact with *Q. stellata* (which occurs on sandy clay or gravel) and, through limited hybridization with the latter, produce *Q. margaretta,* Muller writes: "The ecological circumstance of apparent close agreement between the habitat requirements of *Q. gambelii* stock and the edaphic qualities of the deep sand strips provided a migration route to the Atlantic along the Gulf Coastal Plain. This also provided a buffer against free hybridization with adjacent *Q. stellata* . . . so that gene flow progressed at a retarded rate" (p. 158).

Present-day *Q. gambelii* shows a very wide latitude of edaphic tolerance. Its occurrence has been noted on the following soil types: rich alluvial soil, deep alluvial sand, coarse gravel to sand, shale and clay, sandstone, limestone, schist, quartzite, basalt, andesite, and on a thin layer of volcanic soil overlying limestone. These wide edaphic differences (*Q. margaretta* an obligate inhabitant of deep sand, vs. *Q. gambelii* with very broad edaphic tolerance), at first glance, appear to add to the evidence against a common origin for *Q. gambelii* and *Q. margaretta.*

Their significance might be quite the opposite, however. It is an ecological truism that in a dry climate sand is the wettest possible soil, while in a wet climate it is the driest possible soil. If the migration postulated for ancestral *Q. gambelii had* occurred, this would have been a movement from a relatively dry climate, to a distinctly moister climate (At the present time the Gulf Coast receives decidedly more precipitation than does the range of *Q. gambelii* in the Rocky Mountain region. This relative difference probably obtained during Pleistocene time as well.) The restriction of the ancestral stock (and *Q. margaretta* today) to sand as a form of edaphic compensation

would thus be expected, particularly if it were at a competitive disadvantage on other soil types, or if it were swamped out in such areas by hybridization with *Q. stellata.*

Discussion

In questioning the likelihood of the extensive migration postulated for *Quercus gambelii,* we are not denying that the range of the species extended farther to the eastward during Pleistocene (and perhaps post-Pleistocene) time than at present.

There can be little doubt that life zones were considerably lowered altitudinally (cf. Stearns, 1942), and that various elements of the Rocky Mountain biota (including *Quercus gambelii*) extended somewhat farther eastward then. For example, a number of Rocky Mountain plants (Rogers, 1953) as well as animals (Blair and Hubbell, 1938) reach their present eastern limits in the Mesa de Maya region, which is situated in the southeastern corner of Colorado, the northeastern corner of New Mexico, and the extreme western tip of the Oklahoma panhandle. Their occurrence here, doubtless relictual, is fifty miles or more east of the Rockies. As an even more extreme example, the case of *Peromyscus comanche,* may be cited (Blair, 1950). This species, which occurs along the escarpment of the high plains in the Texas panhandle, is evidently derived from *P. nasutus* (*P. comanche* is regarded as a subspecies of *P. nasutus* by Hoffmeister, 1951), a species ranging widely in the mountains of New Mexico to the west. The two populations must have had a continuous distribution in the past, perhaps as recently as late Wisconsin time, although today they are effectively separated by over 100 miles of barren plains Other instances similar to the above cases could be cited. By the same token, the Pleistocene distribution of *Q. stellata* (and perhaps other elements of the post oak woodland of central Texas and Oklahoma) doubtless extended farther westward than today (cf. Muller, *op cit.:* 154–155).

The two floras—and these two oaks, *Q. gambelii* and *Q. stellata*—may conceivably have come in contact with one another in restricted areas, possibly along major stream courses, such as the Canadian or Cimarron Rivers. Evidence for this, however, has yet to be adduced, and it seems extremely doubtful that there was any extensive migration of either of these oaks beyond any such areas of contact as may have occurred.

As for the origin of *Quercus margaretta,* it is entirely possible that it may have originated from an eastwardly migrating ancestral white oak stock. If this was its origin, however, this migration most likely occurred at some time during early to middle Tertiary. *Quercus gambelii* and *Q. margaretta* are undoubtedly related phylogenetically, but the number and degree of the morphological differences between them suggest a relationship more distant than, and divergence from a common ancestral stock more remote than, say, *Q. gambelii* and *Q. garryana,* of the Pacific Coast. (Leaves, alone, of *Q. garryana* can at times be distinguished only with extreme difficulty —if at all—from those of *Q. gambelii.* This similarity extends down even to trichome morphology.) Close though the relationship may be even between these latter two species, it would seem, nevertheless, that the time of *their* divergence was probably much earlier than Pleistocene—perhaps during Lower Pliocene. It may well have occurred as a concomitant of the Sierra-Cascade uplift and the consequent dessication of the intervening great Basin and Columbia Plateau regions.

Although purely a matter of speculation, the divergence from a common ancestor of the stocks giving rise to *Q. gambelii* and *Q. margaretta* may possibly have followed a pattern similar to that postulated for *Prunus serotina* by McVaugh (1951), and subsequently suggested for a number of other unrelated genera (Mc-

Vaugh, 1952). Following this view, the most likely region from which the ancestral stocks migrated would have been some part of northern Mexico. Of all the North American lobed-leaved white oaks, interestingly enough, *Q. gambelii* is the only one that extends south into Mexico (it occurs along the northern part of both the western and eastern Sierra Madre). Inasmuch as it seems to be less specialized morphologically and ecologically than *Q. margaretta,* moreover, it may possibly be a closer approach to the generalized white oak ancestor from which both species (and perhaps others, such as *Q. garryana* of the Pacific Coast) originated.

As for the subsequent history of *Q. margaretta,* the ultimate solution of the problem will require much additional information. Much more detailed studies are needed of the comparative morphology and anatomy of all the lobed-leaved deciduous white oaks in order to establish a clearer picture of their interrelationships. Clues to past migrations may be provided by fossil deposits—as yet undiscovered—of the early and middle Tertiary in the regions that appear to be critical—the southern Rockies, western Texas, and northern Mexico.

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Appendix

1. Specimens providing bud data presented in figure 1.

Quercus margaretta (voucher specimens in U. C. Herbarium, Davis):

E. O. Beal 2711 1 mi. northeast of Rockfish, Hoke Co., North Carolina
C. R. Bell 5227–1 Salkehatchie River, U. S. Highway 321, Allendale Co., South Carolina
C. R. Bell 5227–2 same
C. R. Bell 5271–1 County Rd. 41, 0.4 mi. east of U. S. Highway 21, Beaufort Co., South Carolina
C. R. Bell 5271–2 same
C. R. Bell 5301 Highway 170, 2.4 mi. north of junction with Highway 128, Jasper Co., South Carolina
C. R. Bell 5331–1 4.9 mi. northwest of Tillman, Jasper Co., South Carolina
C. R. Bell 5347 U. S. Highway 321, 1.5 mi. south of Luray, Hampton Co., South Carolina
C. R. Bell 5381–1 Highway 362, 1.6 mi. south of Padgetts, Colleton Co., South Carolina
C. R. Bell 5381–2 same
C. R. Bell 5381–3 same
W. H. Duncan 20697 3 mi. northwest of Reidsville, Tattnall Co., Georgia
H. J. Jacob 748 just south of Cedar Creek, Highway 63, George Co., Mississippi
G. W. McDowell, Oct. 14, 1956 north side Broad River, Anthony Shoals, Elbert Co., Georgia
G. W. McDowell, Oct. 19, 1956 6 mi. northeast of Patrick, near U. S. Highway No. 1, Chesterfield Co., South Carolina
J. D. Ray, Jr. 7680 7 mi. south of Hattiesburg, Forrest Co., Mississippi
J. D. Ray, Jr. 7681 same
J. D. Ray, Jr. 7682 same
J. D. Ray, Jr. 7683 same
B. C. Tharp No. 1, Nov. 8, 1956 Palmetto State Park, Gonzales Co., Texas

Quercus gambelii (voucher specimens, for all but two, in U. C. Herbarium, Davis):

A. Anderson, Dec., 1956 Dark Canyon, Guadalupe Mtns., Eddy Co., New Mexico (no voucher)
H. S. Haskell, Nov. 22, 1956 Museum of northern Arizona, Flagstaff, Coconino Co., Arizona

H. S. Haskell, Nov., 1956 Highway 89–A south of Flagstaff, Coconino Co., Arizona (no voucher)
R. C. Jackson 2254 entrance to Sandia Park, east side of Sandia Mtns., Bernalillo Co., New Mexico
R. C. Jackson 2255 same
R. C. Jackson 2256 same
J. M. Tucker 2857–9 Phantom Canyon, 5 mi. north of Highway 50, Fremont Co., Colorado
J. M. Tucker 2895–6 Mt. Lemmon, Santa Catalina Mtns., Pima Co., Arizona
J. M. Tucker 2895–11 same
J. M. Tucker 2895–18 same
J. M. Tucker 2895–19 same
J. M. Tucker & H. S. Haskell 2902 19 mi. (by road) north of Young, Gila Co., Arizona
J. M. Tucker & H. S. Haskell 2903 same
J. M. Tucker & H. S. Haskell 2911 ca. ¼ mi. above Lake Mary, beside road to Lake Marshall, Coconino Co., Arizona
J. M. Tucker & H. S. Haskell 2913 slope above Lake Mary, beside road to Lake Marshall, Coconino Co., Arizona
J. M. Tucker & H. S. Haskell 2925 George Wood Canyon, 8 mi. west of Walnut Creek Ranger Station, Yavapai Co., Arizona
J. M. Tucker & H. S. Haskell 2929 beside Senator Highway, ca. 12 mi. (by road) south of Prescott, Yavapai Co., Arizona
J. M. Tucker & H. S. Haskell 2934–7 Butler Wash, 4 mi. north of road from Bluff to Mexican Hat, San Juan Co., Utah
J. M. Tucker 2936–11 Cuba Mesa, ca. 4 mi. northwest of Cuba, Sandoval Co., New Mexico
J. M. Tucker 3010–2 ca. ½ mi. southeast of Highway 166, ca. 8 mi. (by road) southeast of junction with Highway 118, Jeff Davis Co., Texas

2. Specimens from which leaf tracings (fig. 2) were made:

Quercus margaretta:

Top row (left to right)
H. B. Parks, Nov. 19, 1937, Nacogdoches, Nacogdoches Co., Texas (Texas A. & M. Herb. 35671)
A. J. Kirn, Oct. 21, 1935, 2 mi. south of Somerset, Medina Co., Texas (Texas A. & M. Herb. 36139)
H. B. Parks, Sept. 29, 1935, McMahon, Caldwell Co., Texas (Texas A. & M. Herb. 36142)
V. L. Cory 5671, Ottine, Gonzales Co., Texas (Texas A. & M. Herb. 36242)
Second row (l. to r.)
H. B. Parks, Sept. 20, 1934, Sutherland Springs, Wilson Co., Texas (Texas A. & M. Herb. 35901)
Without collector, Cottonwood Swamp, Gonzales Co., Texas (Texas A. & M. Herb. 35855)
H. B. Parks, Oct. 5, 1935, Highway 66 south of San Antonio, Bexar Co., Texas (Texas A. & M. Herb. 35575)
C. H. Muller 8745, 20 mi. south of Mineral Wells, Palo Pinto Co., Texas (S.M.U. Herb.)

Quercus gambelii (All J. M. Tucker collections cited are in the University of California, Davis, Herbarium, but as yet unaccessioned):

Third row (l. to r.)
J. M. Tucker 2855–9, Turkey Creek, El Paso Co., Colorado
J. M. T. 2895–13, Mt. Lemmon, Santa Catalina Mtns., Pima Co., Arizona
J. M. T. 2939–18, 2½ mi. west of Pecos, San Miguel Co., New Mexico
J. T. Marshall, Jr. 37D, west of Colonia Garcia, Chihuahua, Mexico (U. C., Davis, Herb. 14463)
J. M. T. & H. S. Haskell 2864–8, Black Rock Mtn., Mohave Co., Arizona
Bottom row (l. to r.)
J. M. T. 2821–9, Abajo Mtns., 2 mi. west of Monticello, San Juan Co., Utah
J. M. T. 2823–17, ¾ mi. south of Sandstone Ranger Station, Carbon Co., Wyoming
O. M. Clark 10282, Manzano Mtns., New Mexico (Univ. New Mexico Herb. 19005)
J. M. T. 2800–22, mouth of Emigration Canyon, eastern outskirts of Salt Lake City, Utah
J. M. T. 2850–24, Palmer Park, ca. 1 mi. northeast of Colorado Springs, El Paso Co., Colorado

3. Specimens from which trichome drawings were made:

Quercus margaretta:

A. H. H. Bartlett 2560, Wrightsville, New Hanover Co., North Carolina (S. M. U. Herb.)
B. C. H. Muller 8772, 3 mi. north of Rising Star, Eastland Co., Texas (S. M. U. Herb.)
C. C. H. Muller 10130, 1 mi. east-southeast of Carbon, 10 mi. west-southwest of Gorman, Eastland Co., Texas (U. C., Davis, Herb., 22540)

Quercus gambelii (collections in U. C., Davis, Herb.; unaccessioned):

D. J. M. Tucker 2799, mouth of Emigration Canyon, eastern outskirts of Salt Lake City, Utah
E. J. M. T. 3158, 6 mi. north of Pinos Altos, Grant Co., New Mexico
F. J. M. T. 3010–2, ca. ½ mi. southeast of Highway 166, ca. 8 mi. (by road) southeast of junction with Highway 118, Jeff Davis Co., Texas

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DEPENDENCE OF THE ADAPTIVE VALUES OF CERTAIN GENOTYPES IN *DROSOPHILA PSEUDOOBSCURA ON* THE COMPOSITION OF THE GENE POOL

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INTRODUCTION

In a previous publication (Levene, Pavlovsky, Dobzhansky, 1954) we have reported experiments on laboratory populations of *Drosophila pseudoobscura* in which three different gene arrangements were present among the third chromosomes. The adaptive values of six karyotypes (three inversion homozygotes and three heterozygotes) were estimated from the observed changes in the relative frequencies of the gene arrangements in the experimental populations. The results indicated that the adaptive values of at least some of the karyotypes were not constant; they depended upon the presence or absence of certain other karyotypes in the same population. Thus, individuals homozygous for the CH gene arrangement in third chromosome (CH/CH) had a fitness apparently superior to AR homozygotes (AR/AR) in populations in which ST third chromosomes were also present, but CH/CH were inferior to AR/AR in fitness when ST chromosomes were absent. ST homozygotes (ST/ST) were superior to ST/CH heterozygotes in populations which also had AR chromosomes, but ST/CH were superior to ST/ST in the absence of AR.

Lewontin (1955) reported some elegant experiments in which constant numbers of larvae of certain genotypes of *Drosophila melanogaster* were introduced in a limited volume of nutrient medium, and the proportions of these larvae which gave rise to adult flies were recorded. In some instances the numbers of survivors were greater when mixtures of larvae of two different genotypes lived in the same medium than when only one genotype was present. In other words, in these instances a diversity of genotypes facilitated survival. Spiess (1957) has obtained results of rather similar nature in experimental populations of *Drosophila persimilis*. Populations containing third chromosomes with WT and KL gene arrangements, or with WT and MD gene arrangements reach stable equilibria with a predominance of WT chromosomes. However, Spiess' analysis of the selection curves suggests that the relative adaptive values of the karyotypes in these populations are not constant but change as a given karyotype grows more or less frequent in the population. Interestingly enough, experimental populations with only KL and MD chromosomes show no selective changes regardless of which of these chromosomal types is more or less frequent. Spiess correlates this behavior with the fact that WT chromosomes are considerably more frequent in natural habitats than either KL or MD, and thus KL/MD heterozygotes and KL/KL and MD/MD homozygotes are rare in the locality from which the experimental material has been derived.

The experiments to be described below were planned to elucidate further the interdependence of the adaptive values of genotypes which share the same environment. Experimental populations of *Dro-*

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sophila pseudoobscura were made with the same three gene arrangements in the third chromosomes (ST, AR, and CH) which were used in the experiments of Levene, Pavlosky and Dobzhansky (1954). However, the initial frequencies of the different chromosomes in the foundation stocks of the populations were so contrived as to bring out most clearly the interdependence of the adaptive values of the karyotypes present. Moreover, the populations were managed in a way which enabled us to study discrete generations of the flies, rather than overlapping generations as is more usual in experiments with population cages.

The Experiments

The materials and the techniques used were the same as described by Dobzhansky and Pavlovsky (1953) and Levene, Pavlovsky, and Dobzhansky (1954), except for the following detail. The foundation stock of each population (consisting of 2,000 flies of desired genotypes) was placed in a population cage, and kept there for a number of days sufficient for all the 15 cups with the nutrient medium to be inserted in the cage and for numerous eggs to be deposited in all the cups. The cups were then transferred to a fresh cage without any adult flies. When the F_1 adults hatched from most of the cups, samples of the eggs deposited by the F_1 generation flies were taken, and larvae were grown from these eggs under optimal conditions for cytological investigation. The study of these samples permits, then, the estimation of the frequencies of carriers of the different chromosomal types among the flies of the first generation developed in the experimental population. After taking the samples, the flies were allowed to oviposit on fresh cups, which were then transferred to a new cage, where the F_2 flies eventually hatched. Samples of the eggs deposited by the F_2 flies were also taken in most cages for cytological investigation. All the populations were kept at 25° C.

The results of the observations are summarized in table 1. In all, eight populations were studied. Five of them contained the three gene arrangements, ST, AR, and CH, in the third chromosomes. The three control populations, Nos. 134, 137, and 143, contained only AR and CH chromosomes. The pairs of populations, Nos. 132 and 135, 133 and 136, and 134 and 137, were replicates, started simultaneously with similar foundation stocks. Populations Nos. 132–137 were started in December of 1954, and Nos. 142 and 143 were started in March 1955. Each sample whose composition is entered in Table 1 consisted of 300 chromosomes (150 larvae examined cytologically). It is interesting to compare the outcomes of the replicate experiments. Such comparison yields a total chi-square of 5.87 which, for 6 degrees of freedom,

Table 1. *Frequencies (in per cent) of the ST, AR, and CH third chromosomes in the experimental populations*

Population No.	Chromosome	Generation		
		Original	First	Second
132	ST	5.0	14.0	—
	AR	40.0	44.0	—
	CH	55.0	42.0	—
135	ST	5.0	13.7	26.7
	AR	40.0	38.0	41.7
	CH	55.0	48.3	31.7
142	ST	5.0	17.3	28.3
	AR	65.0	59.3	48.0
	CH	30.0	23.3	23.7
133	ST	5.0	14.3	—
	AR	75.0	53.7	—
	CH	20.0	32.0	—
136	ST	5.0	11.3	21.0
	AR	75.0	60.7	60.3
	CH	20.0	28.0	18.7
134	AR	25.0	39.7	46.0
	CH	75.0	60.3	54.0
137	AR	25.0	40.0	46.0
	CH	75.0	60.0	54.0
143	AR	68.0	68.7	66.7
	CH	32.0	31.3	33.3

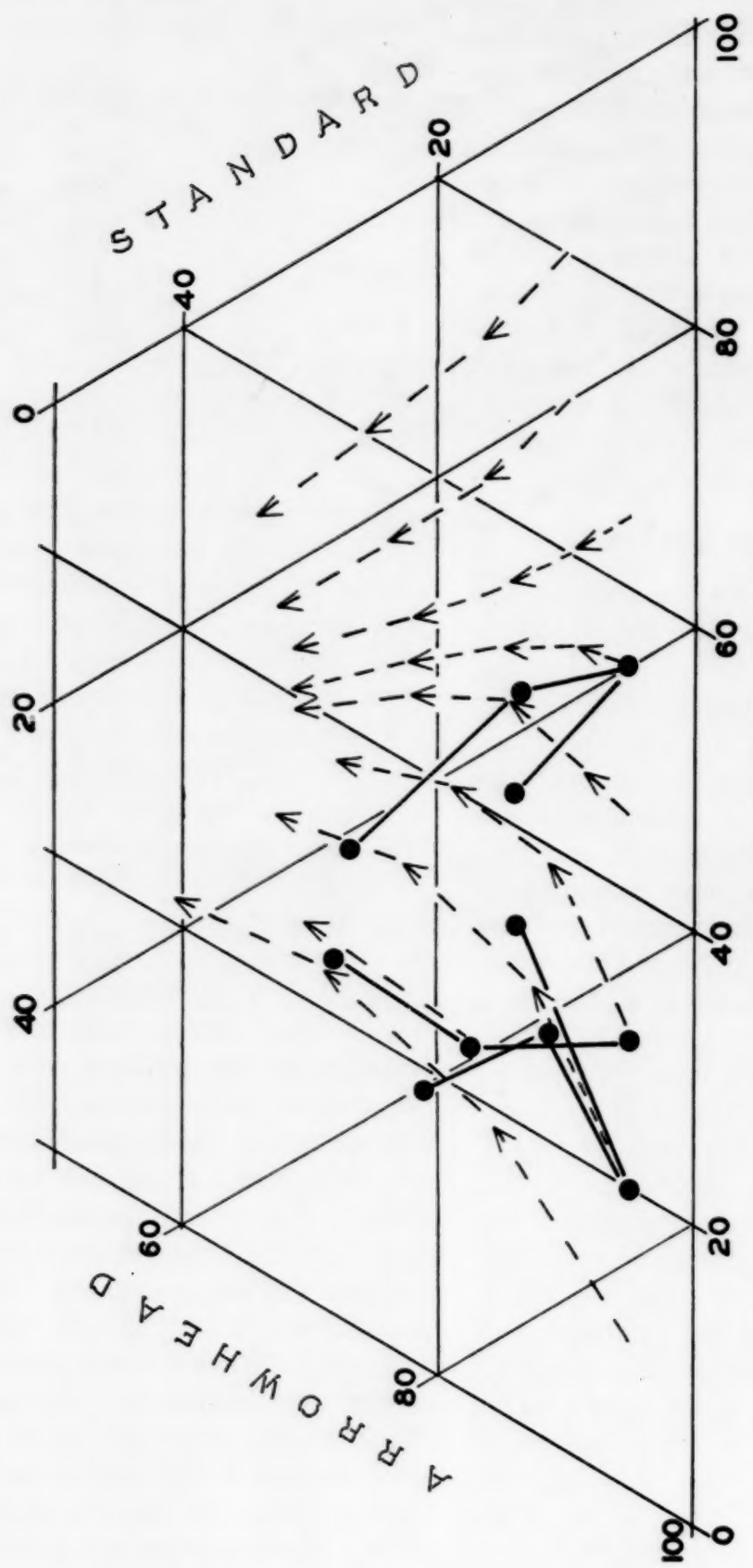

FIG. 1. Chromosome frequencies in per cent. Circles denote starting values (ST = 5 per cent) and values after 1 and 2 generations. Values for the same population are connected by solid lines. Broken lines and arrowheads show the predicted change per generation based on adaptive values from a previous experiment (see text).

corresponds to a probability of between 0.5 and 0.3. Experimental populations of geographically uniform origin thus give reproducible results. This is worth noting since this has been questioned (Epling, Mitchell, and Mattoni, 1953), and also because experimental populations of geographically mixed origin produce results far more variable than can be accounted for by sampling errors (Dobzhansky and Pavlovsky, 1953, 1957).

Analysis of the Experiments

The initial values of the percentages of the three chromosomes in the triple experiments, as well as the subsequently observed values, are plotted on triangular coordinates in figure 1. The observed points are represented by circles, and successive points for the same population are connected by a solid line. Figure 1 also shows a number of dotted lines. Each dotted line segment ending in an arrowhead represents one generation of predicted change under selection, with adaptive values $W_{11} = .83$, $W_{22} = .15$, $W_{33} = .36$, $W_{12} = 1$, $W_{13} = .77$, $W_{23} = .62$, where the subscripts represent the two chromosomes present, with ST = 1, AR = 2, CH = 3. These are the adaptive values estimated from the previous experiment (Levene, Pavlovsky and Dobzhansky, 1954, where the method of plotting is also discussed). It is clear that, except for the first generation starting with 5% ST, 75% AR, and 20% CH (populations 133 and 136), the observed course of events is very different from that predicted from the previous experiment. The value of chi-square for the difference between observed and predicted is 203 with 16 degrees of freedom, far outside the range of the tables. Even recalling that the theoretical adaptive values used were estimated from the previous data, and are subject to some sampling error, it is clear that the two sets of experiments cannot have had the same set of adaptive values.

There are several differences between the two sets of experiments. First, they are separated by two years in time. Second, discrete generations were used in the present experiment, while in the previous one the populations bred continuously, with egg samples being taken at intervals of somewhat more than one generation. Third and most important, the present populations had only 5% of ST chromosomes initially, and 11.3% to 17.3% at the start of the second generation, while the populations reported in the earlier paper had 25% of ST initially, and had over 50% ST for most of the period studied.

Now the previous study led to the conclusion that the adaptive values of AR and CH were evidently reversed in the presence of substantial proportions of ST. But in addition to this, there was some indication that the whole set of five adaptive values changed during the course of the experiment. Specifically, adaptive values calculated for the first 105 days (approximately 4 generations) differed considerably from those calculated from the entire 365 days. Another way of saying this is that the adaptive values became altered as ST rose from a frequency of 25% to one of 80%. The present experiment, involving still smaller percentages of ST, confirms the previous suspicion. However there is one anomalous aspect. One can recalculate the theoretical values shown in figure 1, using the adaptive values $W_{11} = .94$, $W_{22} = .06$, $W_{33} = .51$, $W_{13} = 1.00$, $W_{12} = .48$, $W_{23} = .52$ calculated from the early part of the previous experiment. The resulting arrows move to the right even more markedly than the ones in figure 1, and give an even poorer fit to the observed values. It is not clear why this should be so; however these adaptive values are based on the minimum period of time from which adaptive values can be calculated, and may thus be subject to undue error.

Let us turn now to the analysis of the populations, 134, 137, and 143, contain-

ing only AR and CH chromosomes. The only previous population cage experiment using the same strains of AR and CH as the present one was done by Louis Levine (1955). However, he used small plastic cages and we used larger wooden ones so that the results are not strictly comparable. Taking W_{23} as 1.00, he found $W_{22} = .85$ and $W_{33} = .60$, giving an equilibrium value for AR of $\bar{p} = .73$. The present data are incompatible with these adaptive values, giving $\chi^2 = 38$ with 6 degrees of freedom. The discrepancy is entirely due to the first generation of populations 134 and 137. These two populations, which gave values for AR differing by only 1 fly in 300 in the first generation and exactly alike in the second, went from 25% to 40% AR in 1 generation, compared to a predicted increase to only 31.4%. On the other hand the observed change from 40% to 46% in the second generation compares with a predicted change from 40% to 45%. The lack of significant change in population 143 is also in satisfactory agreement with prediction. All this suggests that in the present experiment there was a generally similar equilibrium value for AR, but more severe selection. Trial and error suggests $W_{22} = .65$ and $W_{33} = .33$, giving $\bar{p} = .66$ and giving $\chi^2 = 1.73$ and $P = .8$, an excellent fit. However, the adaptive values could be as different as $W_{22} = .85$ and $W_{33} = .42$, $p = .79$ without giving a significant chi-square. Nevertheless the present experiment suggests more severe selection, at least against CH, and probably a lower equilibrium frequency for AR than either Levine (1955), using the same strains but somewhat different conditions, or experiments with other strains of AR and CH (Dobzhansky 1948) had suggested.

A more interesting point, but one considerably more difficult to elucidate, is the effect on the relative frequencies of AR and CH of introducing the ST gene arrangement. The present data suggest that the advantage of AR over CH is somewhat reduced in the presence of ST. This could happen in either of two ways. First, taking the adaptive value of the AR/CH heterozygote as our reference point and setting $W_{23} = 1$, W_{22} and W_{33} could remain unchanged by the introduction of ST. Nevertheless, if W_{13} were very large and W_{12} small, CH would be favored over AR in heterozygotes with ST, and would consequently be in a better position relative to AR the more ST chromosomes were present. On the other hand, the presence of flies carrying ST chromosomes might have some ecological effect on flies of karyotypes AR/AR, AR/CH, and CH/CH, actually changing the values of W_{22} and W_{33} relative to W_{23}.

The evidence from the previous experiment (Levene, Pavlovsky and Dobzhansky 1954) was in favor of the second hypothesis, with AR/AR becoming almost lethal. The data from the present experiment is somewhat ambiguous on this point. Preliminary calculations suggest that the data might be fitted reasonably well by the values of W_{22}, W_{23} and W_{33} from the experiment with only two variants present, although the adaptive value of ST/CH would have to be larger than seems plausible. However, since we must suppose that high frequencies of ST in the previous experiment did change W_{22} and W_{33}, it is more reasonable to suppose that they were also changed in the present experiment, but that the low frequencies of ST in the present experiment produced smaller changes in these adaptive values than did the high frequencies of the previous experiment.

Conclusions and Summary

Levene, Pavlovsky and Dobzhansky (1954) studied experimental populations of *D. pseudoobscura* containing initially 25% ST, 25% AR and 50% CH chromosomes from Piñon Flats, California. Within a year the frequencies changed to about 80% ST, 15% AR and 5% CH. The present study used the same strains of flies and the same experimental condi-

tions, except that generations were discrete instead of continuous and that different initial percentages of AR and CH were used. In the present experiments the frequency of ST chromosomes changed from an initial value of 5% to about 28% after two generations. The course of events in the two sets of experiments cannot be explained unless the relative adaptive values of the different karyotypes were different in the two sets of experiments. The most probable cause of this difference was that the frequencies of ST chromosomes were much higher in the first than in the second set of experiments. In our previous study (Levene, Pavlovsky, Dobzhansky, 1954) we concluded that the relative adaptive values of different karyotypes are interdependent. The relative fitness of karyotypes A and B may depend upon the presence in the same medium of other karyotypes, C, D, etc., and upon the actual frequencies of all these karyotypes. The data presented above confirm this conclusion.

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THE BEGINNINGS OF NOMADIC AND GROUP-PREDATORY BEHAVIOR IN THE PONERINE ANTS

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It is a seldom recognized fact that the behavior patterns supposedly characteristic of the doryline "army ants" also occur, at least to a limited extent, in some groups of the primitive subfamily Ponerinae. In the past, entomologists have tended to speak of true army ants as occurring only in the Dorylinae or Leptanillinae, or the Dorylinae exclusively, but it must be admitted that this simple taxonomic qualification is not wholly adequate, particularly in view of the fact that there is now evidence to suggest that the Dorylinae may be polyphyletic (Brown, 1954). The best definition of the expression "army ant" may well be an operational one, of the sort offered by Webster's Unabridged International Dictionary (Second Edition): "Any species of ant that goes out in search of food in companies, esp. the driver and legionary ants." [1]

Actually, the above definition from Webster's Dictionary is incomplete. Upon closer examination one finds that there are really *two* discrete features that may be considered fundamental in army-ant behavior. These diagnostic features can perhaps be most conveniently distinguished under the concepts of "nomadism" and "group-predation." It is my purpose in the present paper to show that both nomadism and group-predation are developed to a variable degree in some genera of the Ponerinae, and that certain species of the genus *Leptogenys* combine these two features to achieve an adaptive "army-ant" type quite similar to that seen in the dorylines. Finally, I wish to take some account of the possible concurrence of nomadism and group-predation in still other groups of ponerines.

[1] There has been a tendency in some recent literature to use the terms "army ant" and "legionary ant" interchangeably. According to Webster's International Dictionary, the term "legionary ant" refers first to the New World army ants of the genus *Eciton,* and second to the "driver ants" of the genus *Anomma.* Most English-speaking authors of the past fifty years have used this term to mean specifically *Eciton* and its relatives, while employing the term "army ant" to cover all of the dorylines, although such application has been far from rigid. In the present paper I have used the two terms synonymously.

Nomadism

Nomadism is a term well entrenched in the myrmecological literature and is probably best defined as *relatively* frequent colony emigration. Most, if not all, ant species shift their nest site if the environment of the nest area becomes unfavorable, and some, e.g., the famous *Iridomyrmex humilis,* are exceptionally restless and normally emigrate one or more times during the course of a single season. But hitherto none have been known in which emigration is undertaken so frequently or accomplished in such an orderly fashion, to cover so much new territory, as in the better known dorylines.

Of supplemental interest is the apparent existence of a limited and aberrant form of nomadism in some members of the ponerine tribe Amblyoponini. W. L. Brown (pers. commun.) has recently called my attention to a peculiar feature of the behavior of the Nearctic species *Amblyopone pallipes* (Haldeman) which certainly points in this direction. Small isolated groups of workers and larvae are often found clustered around recently

killed centipedes, the usual prey of the species. Since the larvae feed directly on the whole centipedes, without previous dismemberment, and since these insects seem too large and clumsy to transport for any distance intact, the suggestion offers itself that the workers transport the larvae to the prey rather than the more normal reverse. It is quite conceivable that colonies emigrate in part or in whole in this fashion to follow their food source.

I have observed similar behavior in the big amblyoponine *Myopopone castanea* (Fr. Smith) in New Guinea. On several occasions small groups of workers and larvae were found clustered about large wood-boring beetle larvae that could not possibly have been carried for any significant distance from the spot where they had been found and presumably killed by the workers. In one rotting log thoroughly dissected by myself, workers and larvae of *Myopopone* were found around two such prey at widely separated spots. The conclusion was inescapable in this case that the colony had distributed itself at least in part to be located near the prey. What constitutes "emigration" in *Myopopone* is open to question, however, since it can be argued that the entire subcortical surface of the log constitutes the "nest" of the ants.

Group-Predation

Group-predation as defined here includes both group-raiding and group-retrieving in the process of hunting living prey. These two processes must be carefully distinguished from each other, since they involve quite different innate behavior patterns and are not invariably linked. Many ant species, particularly those in the higher subfamilies, engage in group-retrieving of prey, but relatively few non-dorylines also group-raid. Various termitophagous ponerines, such as *Leptogenys* of the *processionalis* group and species of *Termitopone, Megaponera, Paltothyreus,* and *Ophthalmopone* (see Wheeler, 1936), do group-raid and are in this sense truly group-predatory. The Cerapachyinae, which appear to be primarily or exclusively robber ants (myrmecophagous), also include truly group-predatory species, a point I have developed at length in another paper on the biology of this group (Wilson, 1958). True group-predation is not to be confused with the specialized form of group-raiding conducted by the slave-making ants, including *Polyergus, Rossomyrmex, Strongylognathus,* and members of the *Formica sanguinea* group, which are specialized parasites hunting live captives rather than prey.

The Ponerine Army Ants

Now the very important question must be raised: To what extent are nomadism and group-predation associated in the non-doryline ants? Unfortunately, only a very incomplete answer can be supplied to this question, since we are handicapped by a scarcity of information on the extent of nomadism, or for that matter, emigration of any sort, in most ant groups. Perhaps it is sufficient at this point to establish the fact that the association of nomadism and group-predation, constituting at least the most general characteristics of true "army-ant" behavior as defined here, does exist in the Ponerinae. Below are given two examples from the genus *Leptogenys*[2] recently studied by present author in New Guinea, followed by a selection of probable and likely cases from other ponerine genera.

Leptogenys diminuta (Fr. Smith)

This species, belonging to the *L. kitteli* group and ranging from Ceylon and Botel Tobago to the Solomons and Queensland, was collected by the author in the following localities in eastern New Guinea: Karema, Brown River (accession no. 539); Bisianumu, 500 m. (acc. nos. 608,

[2] Group-predation *sans* nomadism is already a well-known phenomenon in the *processionalis* and *kitteli* groups of *Leptogenys*. The reader is referred to summaries of information on this subject by Wheeler (1910, 1936).

644, 659); Nadzab, Markham Valley (acc. nos. 1087, 1106, 1107); Bubia (acc. no. 1059); lower Busu River (acc. nos. 934, 940); Mongi River near Sambeang. On several occasions estimates of colony size and composition were made, and are given below:

1. *Acc. no. 1087.* May 20–22, 1955. Seventy to eighty workers, 10 males, and an undetermined amount of brood, consisting of larvae, one-quarter to full grown, and cocoons, the latter predominating.

2. *Acc. no. 1106.* May 20–22, 1955. One ergatogyne (highly ergatoid), about 150 workers, 10 males, and an undetermined amount of brood, consisting of larvae, one-half to full grown, and cocoons, the latter predominating.

3. *Acc. no. 539.* March 8, 1955. Somewhat in excess of 300 workers.

4. *Acc. no. 608.* March 15–20, 1955. About 200 workers and several males.

L. diminuta is one of the most widely ranging of New Guinea ponerines, occurring in dry evergreen forest as well as in rainforest at various elevations. It seems to favor forest borders and partial forest clearings. The nests are very temporary in aspect, consisting of nothing more than preformed cavities in rotting logs or simple bivouacs in open leaf litter. There is no evidence of excavation or nest building of any kind. Mann (1919) made the same observation with respect to this species ("var. *santschii*") [3] in the Solomons: "On several occasions I found masses of workers, accompanied by males, swarming on the ground, always in the forest, and numerous larvae and pupae beneath pieces of bark on the ground. Probably these were temporary nesting places." Neither Mann nor I observed actual colony emigration in this species, but Mann noted what was undoubtedly this process in a closely related, undescribed species from Malaita (Mann, 1919; cited erroneously as "var. *laeviceps*").

Group-predatory behavior, involving the essential process of group-raiding, as well as group-retrieving, is markedly developed in *L. diminuta.* At a lumbering camp on the edge of the Busu River, near Lae, New Guinea, where I stayed during May, 1955, I watched the workers of a *diminuta* colony forage in groups on two successive days. On both occasions approximately forty workers, forming a short, compact column of three to six individuals in width, emerged during late afternoon from the dense grass of a forest clearing out onto the bare ground surrounding an open firewood hut. As in dorylines, group cohesion was strong, each worker appearing unwilling to leave the file to forage on its own. Leadership of the group changed constantly from one worker to another. After a few minutes of exploration in this open space, the current of movement turned, and the group began to press back toward the grass border. One afternoon a secondary file was found ascending the supporting poles of the hut rafters. Here group cohesion was less marked than on the ground, and some of the workers ventured out singly for short periods of time. Nearby, in the Busu rainforest, a group of workers from another colony were found during mid-morning foraging together around the base of a tree.

Food-retrieving in this species also entails extensive group activity, at least where large prey are involved. At the rainforest border near Bubia, also near Lae, about nine o'clock in the morning, six to ten workers were found carrying a rather large beetle larva together; they were all moving fairly easily in the same direction. No other workers were in evidence in the immediate vicinity. In the primary lowland rainforest near Karema, Papua, several hundred workers were found group-retrieving a very large millipede. They were first encountered at eight o'clock in the morning, when the first rays of sunlight were beginning to

[3] The formal synonymy of Mann's var. *santschii,* along with other proposed taxonomic changes in *Leptogenys,* is planned as part of the author's forthcoming revision of the Melanesian Ponerinae.

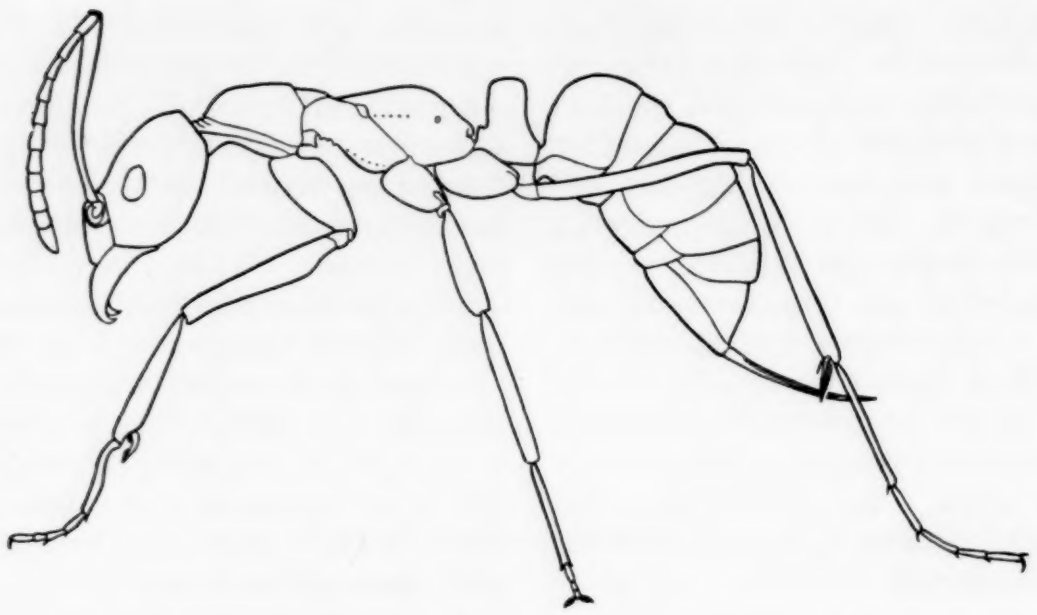
reach the forest floor. Large numbers of the workers were streaming back and forth between the millipede and the bivouac site, a distance of about five feet. The millipede was very feeble, but still alive and able to move slowly under its own power, despite the hindering action of the masses of ants which covered and pulled at it. By 9:00 it had moved to a point six feet from the nest. By 9:30, however, it was completely immobilized, and the ants had dragged it back to the five foot mark. By 10:30 they had dragged it all the way back to the nest site and covered it with leaf litter.

Leptogenys purpurea Emery

This is a second species of the *L. kitteli* group found on New Guinea. In the eastern part of the island it has been collected from sea level to 1,500 meters, and is apparently most abundant in the upper part of this elevational range, from about 800 to 1,500 meters. I encountered it on several occasions during a trip through the mountainous region around the headwaters of the Mongi and Mape Rivers, in the eastern part of the Huon Peninsula. The observations recorded below form the basis for my conclusion that this species shows nomadic and group-predatory behavior.

Near Tumnang (1,500 m.) a colony emigration of *L. purpurea* (accession no. 803) was discovered in progress at 12:30 P.M., just as the early afternoon mists were closing in on this mountainous area. What seemed to be the advance workers had made their appearance, forming a loose file which emerged from the impenetrably dense grass of a forest clearing onto a native trail, followed the open ground of the trail for about eight feet, and then turned off into the grass again. During the next thirty minutes a large number of workers, roughly estimated to be 2,000, emerged and passed along this route. At full strength the column they formed was tightly packed and measured about six individuals across. In its swift movement and compact structure this column strongly reminded me of the raiding columns of the larger ecitonines I have observed in tropical Mexico. Single *Leptogenys* workers periodically left the column and moved for several inches to a foot to the side behore returning to the main stream. These individuals were very aggressive and readily attacked objects offered them; in effect they were functioning as scouts or guards for the emigrating colony. Large numbers of workers were constantly returning against the main current and may have been on their way back to the original nest site to pick up additional brood. As many as 1,000 cocoons, along with a few mature to nearly mature larvae, were passed along in the course of the emigration. Unfortunately, only two of the cocoons were preserved; upon later dissection one was found to contain a partially pigmented worker pupa and the other an early prepupa of indeterminate caste. At least ten fully colored males also passed in transit; in each case they were being carried along (with their appendages folded up in "pupal" posture) by workers. A few callow workers were also present; these were moving on their own power and made their appearance toward the end of the emigration. The only food being transported was a fragment of a grasshopper, carried by a single worker. Despite careful scrutiny of the column, no female reproductive was sighted, although it is admitted that a worker-size ergatogyne might easily have been overlooked.

At Gemeheng, a colony of *purpurea,* containing at least a thousand workers (acc. no. 781), with a large quantity of brood, was found in a bivouac in the lower strata of a pile of recently cut grass and brush in a clearing in mid-mountain rainforest. At 10 A.M., during a clear, sunny morning, two independent columns of workers were proceeding out in different directions, and could be followed through the grass for distances of about six feet. One column was bringing in a large carabid larva, while the other



Worker of the ponerine ant *Leptogenys purpurea* Emery; Gemeheng, N.-E. New Guinea (acc. no. 781).

was apparently pushing out in the initial stage of foraging. Movement to and from the bivouac site was at this time about balanced. In the bright sunshine these tightly organized, fast-moving lines of metallescent ants made a striking sight. Their brood consisted of mature to nearly mature larvae and cocoons. Two of the cocoons were preserved and later dissected; both contained male pupae.

Near Wamuki, on the Mongi headwaters, about 500 workers were found nesting in a large preformed cavity in a rotting log on the floor of foot-hills rainforest. At midmorning, when the colony was discovered, a column of workers, apparently in the act of foraging, extended out from the log for a distance of about six feet.

Genus *Onychomyrmex*

Members of the aberrant amblyoponine genus *Onychomyrmex* resemble dorylines in many ways, leading W. M. Wheeler (1916) to suggest that "it is not improbable that the colonies move from place to place in search of their prey, like the colonies of the subterranean Dorylinae (*Eciton coecum* and *Dorylus*), which they very closely resemble in behavior, color, sculpture, and pilosity." Information on the habits of *Onychomyrmex*, a genus confined to the rainforest areas of northern Queensland, is still very limited. Wheeler found workers of *O. hedleyi* group-foraging on two occasions, and of *O. mjobergi* says, "The ants moved rather slowly in long files through cracks in the wood [of rotting logs], evidently endeavoring to keep in close touch with one another by means of their antennae, after the manner of the Dorylinae."

These observations have been confirmed by W. L. Brown (pers. commun.), who studied *O. hedleyi* and *O. doddi* in the field in 1950. He found large numbers of workers moving in compact files without brood through rotting logs, evidently in the process of group-foraging. He was particularly impressed by the rapid, doryline-like vibration of the antennae by which the workers kept in touch with one another. Unfortunately, neither Wheeler nor Brown were able to make definitive observations on the frequency of colony emigration, and the existence of nomadism in this genus must be considered purely suppositional.

Megaponera foetans (Fabr.)

The group-predatory behavior of this giant termitophagous species has been described by several authors independently

(see in Wheeler, 1922, 1936). In 1914 Arnold discovered a colony in emigration and was able to extract the reproductive female, which turned out to be an ergatogyne. The elaborateness of the emigration witnessed by Arnold, involving as it did the utilization of several "way stations," together with the circumstance that *M. foetans* evidently lives exclusively on a diet of termites, caused Wheeler (1936) to suggest that this species leads a nomadic life, i.e., constantly shifts its nest site to locate near fresh termite colonies. Much the same considerations apply to the other large, group-foraging, obligatorily termitophagous ponerines, such as *Termitopone* and *Ophthalmopone,* although unhappily we know even less about the biology of these forms than in the case of *Megaponera* (Wheeler, 1910, 1936).

Genus *Simopelta*

Simopelta is another ponerine genus whose members may eventually be found to qualify as true army ants.[4] The reproductive female of *S. pergandei,* recently described by Borgmeier (1950), is a dichthadiiform ergatogyne extraordinarily convergent to that found in the dorylines. Although this and other species of the genus occur widely through the New World tropics and have been collected repeatedly, virtually nothing is known of their habits. We have only the following suggestive statement by Mann (1916) concerning *S. jeckylli:* "The type colony was discovered quite accidentally, by scratching away some of the leaves and debris with which the ground in the forest is everywhere covered. As far as I could ascertain the ants were travelling in a definite direction."

[4] It is noteworthy that in at least one species of the closely related genus *Belonopelta* (*B. deletrix*) the workers forage solitarily and the reproductive female is a normal, alate queen (Wilson, 1955). No information is available on emigration frequency.

The Adaptive Value of Legionary Behavior

The combination of nomadic and group-predatory behavior has been achieved on at least two separate occasions in the evolutionary history of the ants: in the Dorylinae and in the ponerines of the *Leptogenys kitteli* group. It has been commonly assumed (but never proven) that the Leptanillinae are legionary, and if this is true these aberrant little ants undoubtedly represent a third independent army ant group. Finally, if the Dorylinae are diphyletic or triphyletic, as Brown (1954) has suggested, and if the members of *Onychomyrmex, Megaponera,* and *Simopelta* are both nomadic and group-predatory, as suggested here, then army-ant behavior must be considered to have arisen separately a minimum of seven times. This circumstance, coupled with the fact that the Dorylinae, which represent the ultimate in the army ant trend, are so eminently successful in tropical regions all over the world, indicates that legionary behavior confers a considerable selective advantage.

The adaptive value of nomadism seems abundantly clear. By continually moving into fresh hunting grounds, exclusively predatory ants are able to build up relatively large colonies (Wheeler, 1910). Schneirla (1956) has described how the great columns and swarms of *Eciton* strip the rainforest floor of much of its arthropod fauna during mass forays. These ants could not long survive if confined to the narrow trophophoric fields occupied by sedentary ants.

The selective advantage of group-predation is a matter of somewhat greater complexity. It has been noted repeatedly that compact armies of ants are more efficient at flushing and capturing prey than assemblages of lone foragers, and this is certainly a correct observation, but it is not the whole story. In my opinion there is another, primary function of group-predation that becomes clear only when the food habits (prey preference)

of the group-predatory ponerines, cerapachyines, and dorylines are compared with those of the ponerines that forage in solitary fashion. The great bulk of non-legionary ponerine species of which the food habits are known take living prey of approximately the same size as their worker caste or smaller. As a rule they depend on proportionately small animals which can be captured and retrieved by lone foraging workers. Group-predatory ants, on the other hand, normally include large arthropods or the brood of other social insects in their diet, prey not normally accessible to solitary foraging ants. Thus *Leptogenys diminuta* and *L. purpurea* seem to specialize on large arthropods, *Eciton* and *Anomma* species prey on a wide variety of arthropods, including social wasps and other ants, *Megaponera foetans* specializes on termites, cerapachyines specialize on other ants, and so forth. It seems quite probable that group-predation, and with it the broader pattern of army-ant behavior, has arisen generally as a coadaptation to predation on large arthropods and social insects.

The Early Evolutionary Stages of Legionary Behavior

Thanks to the persistently conducted and exhaustive researches on *Eciton* by Schneirla and his associates (1956, 1957, and contained references), we now know perhaps more about the biology of this genus than about that of any other group of ants. A promising start has also been made on the African doryline genus *Anomma* by Raignier and van Boven (1955). But as enlightening as this work has proven to be throughout its many biological and ethological ramifications, there is still one important subject on which it has been unable to throw much light, and indeed cannot be expected to, and that is the early evolutionary history of army-ant behavior. To observe the beginnings of nomadism and group-predation, and the association of these two features to form true legionary behavior in a primitive state, we must leave behind the highly specialized dorylines and go to the Ponerinae. There are admittedly great gaps in our present knowledge of ponerine behavior, particularly with reference to the causal mechanisms behind foraging and emigratory activity, and it is impossible at this stage to speak about evolutionary trends with any degree of precision. Nevertheless, the point has been reached where it is at least possible to formulate a working hypothesis of the phyletic development of legionary behavior in terms of major adaptive steps. In the author's opinion, four such steps can be conceived, as follows:

1. *Group-predation is developed to allow specialized feeding on large arthropods and other social insects.* Group-predation without nomadism may occur in some of the cerapachyine ants, e.g., *Cerapachys* (*s. str.*) and *Phyracaces* (cf. Wilson, 1957), but this is probably a short-lived step, soon giving way to the stage described below.

2. *Nomadism is either developed concurrently with group-predatory behavior, or is added shortly afterwards.* The reason for this new adaptation is that large arthropods and social insects are more widely dispersed than other types of prey, and the group-predatory ant must constantly shift its trophophoric field to exploit these new food sources. With the acquisition of both group-predatory and nomadic behavior, the species is now truly "legionary" in the operational sense adopted here. Most of the group-predatory ponerines are believed to have reached this adaptive level. Colony size in these species averages larger than in related, non-legionary species, but does not approach that attained by *Eciton* and *Anomma.*

3. *As group-predation becomes more efficient, prey preference is expanded to include smaller, non-social insects and other arthropods.* The species tends to become a general predator showing little

prey discrimination. Colony size remains intermediate. No examples of this hypothetical intermediate stage are known at present, but some of the more poorly studied group-predatory ponerines may well prove to belong here.

4. *As the group-predatory and nomadic faculties are further improved, large colony size becomes possible.* This is the stage attained by most or all of the Dorylinae.

In the present paper, I have made an attempt to focus attention on what I have considered to be affirmed and probable examples of army ants in the Ponerinae. Whether or not my interpretations, theoretical and otherwise, prove correct in particular cases, I hope that I have at least succeeded in establishing the importance of extending studies of ponerine biology with this point of view included.

Summary

Army-ant (legionary) behavior is characterized by the combination of two discrete features, nomadism and group-predation, both of which are maximally developed in the subfamily Dorylinae. A growing body of evidence indicates that similar behavior, manifested at least in rudimentary form, has been evolved independently on several occasions in the more primitive subfamily Ponerinae.

An examination of the fragmentary information available on the biology of the various legionary and pre-legionary ponerines has led to the formulation of the theory presented herein, that group-predation has been evolved initially as a coadaptation to specialized feeding on large arthropods and social insects, while nomadism has been evolved secondarily to allow more efficient exploitation of this relatively widely dispersed food source. Later evolutionary steps, exhibited by the higher Dorylinae, have included the wide extension of prey preference and the increase of normal colony size.

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EXPERIMENTAL STUDIES OF MIMICRY IN SOME NORTH AMERICAN BUTTERFLIES

PART I. THE MONARCH, *DANAUS PLEXIPPUS*, AND VICEROY, *LIMENITIS ARCHIPPUS ARCHIPPUS*[1]

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INTRODUCTION

When the vast literature on mimicry is considered, the striking lack of experimental evidence for its existence is remarkable. Morgan (1896, 1900), while studying learning in chicks, designed mimicry experiments which showed that they can associate an unpleasant feeding experience with a particular color and pattern. Thereafter, the chicks would also reject modifications ("mimics") of the same color pattern. More recently, Mühlmann (1934) used dyed and treated mealworms as "models," and partially dyed ones as "mimics" in experiments with several species of passerine birds in an attempt to show how similar a model and mimic must be to deceive the birds. The work of Mostler (1935) on wasp-mimicry showed that birds could learn to reject wasps, and then also would mistake like-colored insects for wasps and reject them. Working on the problem of beetle mimicry, Darlington (1938) carried out experiments with captive *Anolis* lizards, which showed that they rejected the model beetle, and also mimic beetles. The laborious efforts of Finn (1895, 1896, 1897a, 1897b), Marshall (1902), Pocock (1911), Swynnerton (1919), Carpenter (1921, 1942), and Jones (1932) are paramount among the many attempts to determine the relative edibility of mimetic butterflies to various vertebrate predators. Both Marshall and Swynnerton reported some evidence for the existence of mimicry in the complex African butterfly fauna, on the basis of feeding experiments with captive Baboons and captive Rollers (*Coracias garrulus* Linné) respectively, but the major parts of both works were devoted to the more general problem of cryptic *versus* warning coloration in butterflies.

As Poulton (1909) pointed out, in North America there are three relatively simple examples of supposed mimicry in butterflies. The purpose of the present study is to describe an experimental investigation of mimicry in these North American butterflies, and it will be presented as three papers which deal separately with each of these three mimicry complexes. The same methods were employed for each complex, and the three parts were carried out as a continuous investigation over a period of 60 days. The first series of experiments was carried out with *Danaus plexippus* (Linné) and *Limenitis archippus archippus* (Cramer), presumed model and mimic, respectively. *D. Plexippus* is known respectively as the Monarch and *L. a. archippus* is known as the Viceroy; they will hereafter be referred to by their common names. The second series of experiments was a study of the model, *Battus philenor* Linné, and its mimics, *Papilio troilus* Linné, *P. polyxenes* (Fabricius), and the black female form of *P. glaucus* Linné. The third series was a study of the model, *Danaus gilippus berenice* (Cramer), and its mimic, *Limenitis archippus floridensis* (Strecker). The

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experiments were designed to investigate the following relationships between models and mimics and a selected bird species, to be used as a caged predator:

1—the reaction to models by individually caged experimental birds;
2—the reaction to mimics by the same experimental birds, after they had had initial laboratory experience with the models;
3—the reaction to mimics by individually caged control birds, which had had no prior laboratory experience with the models.

An experimental study demonstrating these three points could be expected to show the effectiveness of mimicry, within the limitations of the experimental conditions.

Materials and Methods

The technical difficulties inherent in these experiments were minimized by the choice of an especially favorable situation in which to undertake the investigation. The Archbold Biological Station, near Lake Placid, Florida, provided excellent laboratory facilities, without which the work would have been impossible. In addition the required butterflies are relatively abundant in this area of Florida.

The Florida Scrub Jay, *Cyanocitta coerulescens coerulescens* (Bosc), was selected as the predator in the mimicry experiments. It is non-migratory and is found in areas in which Sand Pine (*Pinus clausa* (Engelm.) Vasey), scrubby oaks (*Quercus myrtifolia* Willd., *Q. geminata* Small, and *Q. catesbaei* Michx.), Saw Palmetto (*Serenoa repens* (Bartr.) Small), and Dwarf Wax Myrtle (*Myrica pumila* Michx.) predominate (Bent, 1946, and Amadon, 1944). The diet of the Scrub Jay is said to be about 60% animal matter, on the basis of analyses of stomach contents of sixteen birds (Bent, 1946), and includes beetles, butterflies, moths, caterpillars, and grasshoppers. Sprunt (1954) stated that the animal matter is 50% and did not note the presence of Lepidoptera in the stomach contents. Amadon (1944) observed Scrub Jays feeding in nature at the Archbold Biological Station, primarily on acorns and insects. The male and female Scrub Jays have similar plumage and size, though the males may be slightly brighter in color and larger than the females. Amadon also observed that in his experience a hiccup sound is peculiar to the female Scrub Jay. These birds are particularly easy to trap, and readily adapt to life in a cage (Amadon, 1944, and Bent, 1946).

Eight Florida Scrub Jays were trapped on the Archbold Biological Station property between 14 April and 17 April 1956. Since the young are known to hatch in early to mid April, it may be assumed that these Scrub Jays were all at least one year old. As noted above, the sex of these jays is difficult to determine from plumage, and even from size. However, in an attempt to ascertain the sex of the nine individuals used in the experiments, all but one were weighed prior to release. The following weights were recorded on 17 June 1956:

No. of bird	Weight in gms.	Tentative sex determination
C-1	84.0	male
C-2	66.5	female
C-3	83.0	male
C-4	77.0	female (hiccup)
E-1	88.0	male
E-2	74.0	female (hiccup)
E-3	71.0	female
E-4	—	mate of E-3
E-4A	77.5	female

From a generalization based on weight alone, C–2, E–3, and E–4A (a replacement for E–4, captured 1 June 1956) seemed to be females. E–4, the probable wild mate of E–3, was not weighed prior to release. On the basis of the hiccup sound mentioned by Amadon (1944), C–4 and E–2 could be considered females. C–1, C–3, and E–1 could have been males.

Each bird was confined in a cubic cage thirty inches on a side, with sides and top covered with aluminum-painted wire of

one-half inch square mesh. The cages were arranged in the laboratory in two racks of four each, within two adjacent enclosures 6′ wide × 13′ 5″ deep × 7′ 8″ high. Each enclosure had a door (3′ 6″ wide × 7′ high) at one end, and both the door and the top of each enclosure were made of one-half inch square mesh. The eight bird cages were identical in every possible respect, as were the two enclosures. The individual bird cages were separated from one another by opaque cardboard, so that at no time could one bird see another. In each enclosure there was a pair of white porcelanized reflectors, each with a 100 watt incandescent bulb, fastened on the wall opposite the rack bearing the cages. These lights were on during all the experiments, and off when experiments were not in progress. Daylight entered the laboratory through a large skylight of northern exposure. The aluminum-painted steel tray floor of each of the eight bird cages was covered with sifted white sand obtained from the area where the birds were caught. Two perches at heights of 8″ and 16″ were provided in each cage, and each had a water bottle accessible at all times.

The eight birds were given a regular feeding at 5:30 P.M. daily. The standard laboratory diet consisted of approximately: 5 cc scratch (cracked corn and wheat), 1 cc pebbles, 2 cc Purina chow (for hens), 2 pecan meats, 1 peanut, 2 sunflower seeds, and 4 Scarabaeid beetles (*Phyllophaga prununculina* Burmeister). Occasionally, one or more additional items were given simultaneously to all birds. These included hard boiled egg, egg shell, lettuce, chopped meat, bread, and insects of various orders.

Experimental Insects

Insects of the orders Coleoptera, Hemiptera, Orthoptera, and Lepidoptera were attracted by a 15 watt G-E black light stationed on an outside platform of the laboratory. These were collected each night and stored in a cold room (about 3° C.) for use in the feeding experiments with the Scrub Jays. It is of interest that wild birds, including the Florida Scrub Jay, fed regularly at dawn on the remaining insects that had been attracted to the light the night before. The butterflies used in the experiments were obtained by collecting in the field, or by rearing the adults from eggs laid by confined female butterflies, or from larvae found in the field and reared in the laboratory. Supplies of butterflies were also stored in glassine envelopes in the cold room for use as needed. The particular source of each species will be noted as the experiments are described. No effort was devoted at this time to a study of the proportions of models and mimics in given localities.

Preliminary Experiments

To determine whether or not any eratic behavior existed among the eight Scrub Jays, all of the birds were given identical preliminary tests with several orders of insects. All birds responded similarly to representative Coleoptera (e.g., *Phyllophaga prununculina* and *Dyscinetus morator* Fabricius, Scarabaeidae, *Epicauta tenuis* (Leconte), Meloidae); Orthoptera (e.g., Acrididae, and *Gryllotalpa hexadactyla* Perty, Gryllidae); Hemiptera (e.g., *Lethocerus uhleri* (Montandon), Belostomatidae); and Lepidoptera (e.g., *Pholus fasciatus* (Sulzer) and *Xylophanes tersa* (Linné), Sphingidae; *Phoebis sennae eubule* (Linné), Pieridae; *Papilio glaucus* Linné (yellow female and male), *P. palamedes* (Drury), and *P. marcellus* (Cramer), Papilionidae). In each trial for each bird, a stopwatch was used to record the time in seconds for the bird to seize an insect, and if the bird then ate the insect, this time was also recorded. Similarity among all the birds in their reaction times in seizing the insects, and also in their responses to the insects after seizure, indicated that they were a reasonably uni-

form group with which to conduct experiments on mimicry. The set of mean reaction times, based on twelve trials for each of the eight birds, gave an observed standard deviation of 1.34 seconds, with a mean value of 3.31 seconds and a range of from 1.5 to 5.0. A table in David, Hartley, and Pearson (1954) showed that for eight observations the ratio of range to standard deviation must be 3.399 at the 5% significance level; the ratio of range to standard deviation here is 2.61 so that there is no significant difference among the eight observations, i.e., the birds' mean reaction times in seizing insects.

During the preliminary trials, two readily available butterflies, *Papilio glaucus* (yellow female and male) and *P. palamedes* which are not known to be involved in mimicry either as models or as mimics, were eaten in every case by all eight birds. It was therefore decided that these two species, obtained as living adults by local field collecting, would be used as the edible control butterflies throughout the course of the experiments. Hereafter they will be referred to as "non-mimetic butterflies." In all of the experiments the butterflies were immobilized by pinching the thorax before they were placed with a pair of forceps on the floor of a bird cage. For uniformity and stability all butterflies were presented lying on their sides, with wings together dorsally. Therefore in the experiments with models and mimics only mimicry in the characters of the underside of the wings was being tested. The immobilization of the butterflies and their sideways placement in the cages were arbitrarily decided upon to eliminate the following variables: (1) a mobile butterfly might be more or less difficult for a bird to catch depending on its amount of activity and its location in a cage; (2) mimicry might be more or less effective depending on whether a bird saw the upper or lower wing surfaces of a temporarily resting butterfly, or both surfaces of a flapping butterfly. The role of behavior of models and mimics in increasing or diminishing the effectiveness of mimicry would be interesting in itself (e.g., it is known that two forms of the African butterfly, *Hypolimnas dubius* de Beauvais, which mimick two closely allied *Amauris* models, differ from one another in behavior as well as color and pattern, as discussed by Ford, 1953), but the present experiments do not attempt to investigate this aspect of the problem. Every bird was allowed two minutes to react to each butterfly presented. At two minutes an uneaten butterfly was removed. Whenever possible, living butterflies were used, but the data indicated that the reaction to any given species of butterfly was the same whether live or dead specimens were presented to the birds. In a few trials, dead and rather dried specimens, of non-mimetic butterflies only, had to be used, and rarely a slightly moldy non-mimetic butterfly was used in the absence of fresh material. Even these butterflies were quite acceptable as food to the jays. If a living model or mimic remained untouched throughout a trial, it was used again in successive trials. If a model or mimic was in any way torn or injured by a bird, however, it was not used again.

The Mimicry Experiments

Of the eight Scrub Jays, four were randomly selected as experimental birds; the other four were control birds. The mimicry experiments were designed so that each trial consisted of giving a bird a pair of butterflies in succession, one non-mimetic butterfly and one model or one mimic. In each trial, the order of presentation of the non-mimetic butterfly and the model or mimic was determined by a random number table, with the use of consecutive digits in a different vertical column for each bird. If a digit read 0–4, a non-mimetic butterfly was given first, followed by a model (or mimic), but if a digit read 5–9, a model (or mimic) was given first, followed by a non-mimetic butterfly. By this method

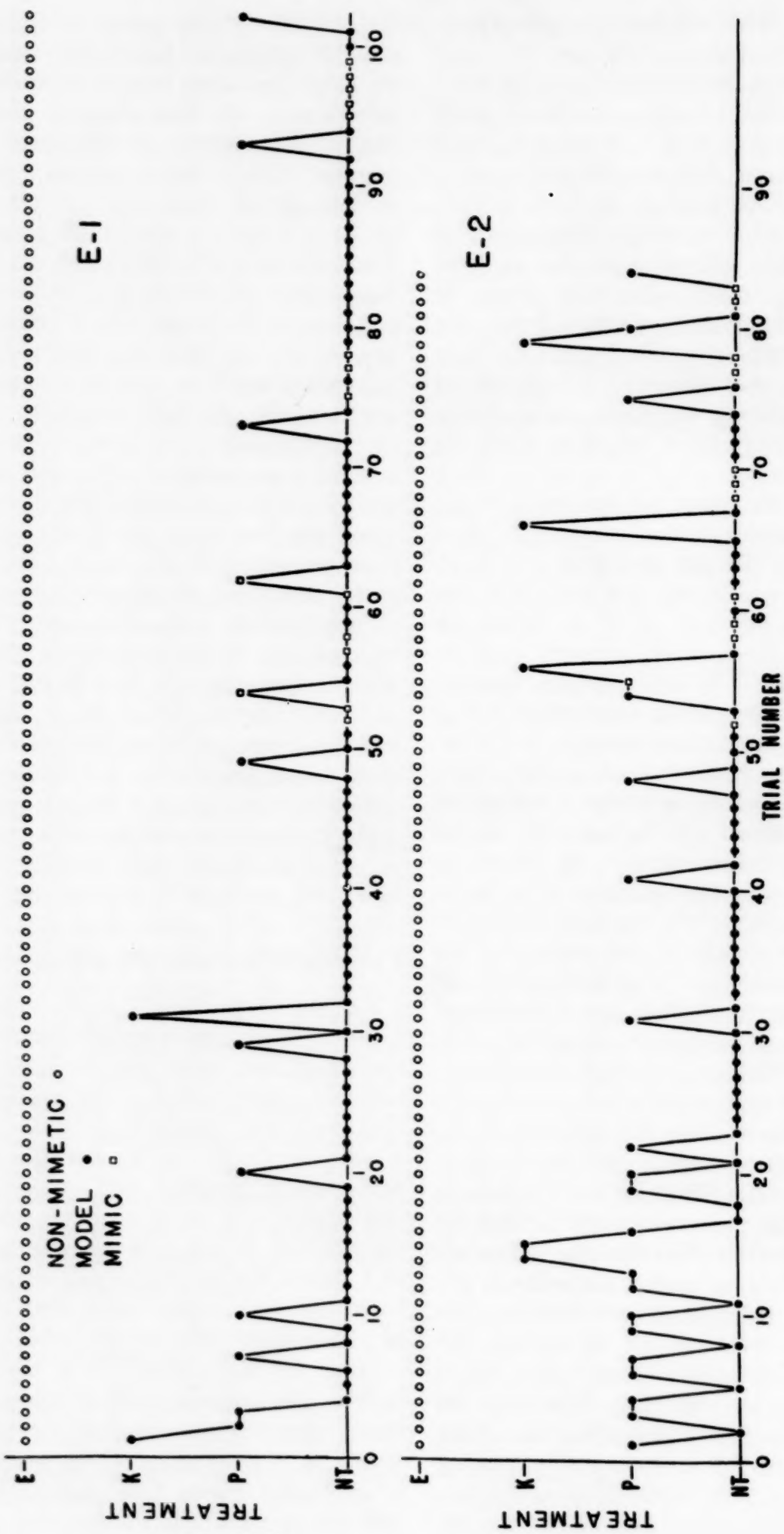

FIG. 1A. Diagrams for experiments with the Monarch and the Viceroy. Experimental birds E-1 and E-2.

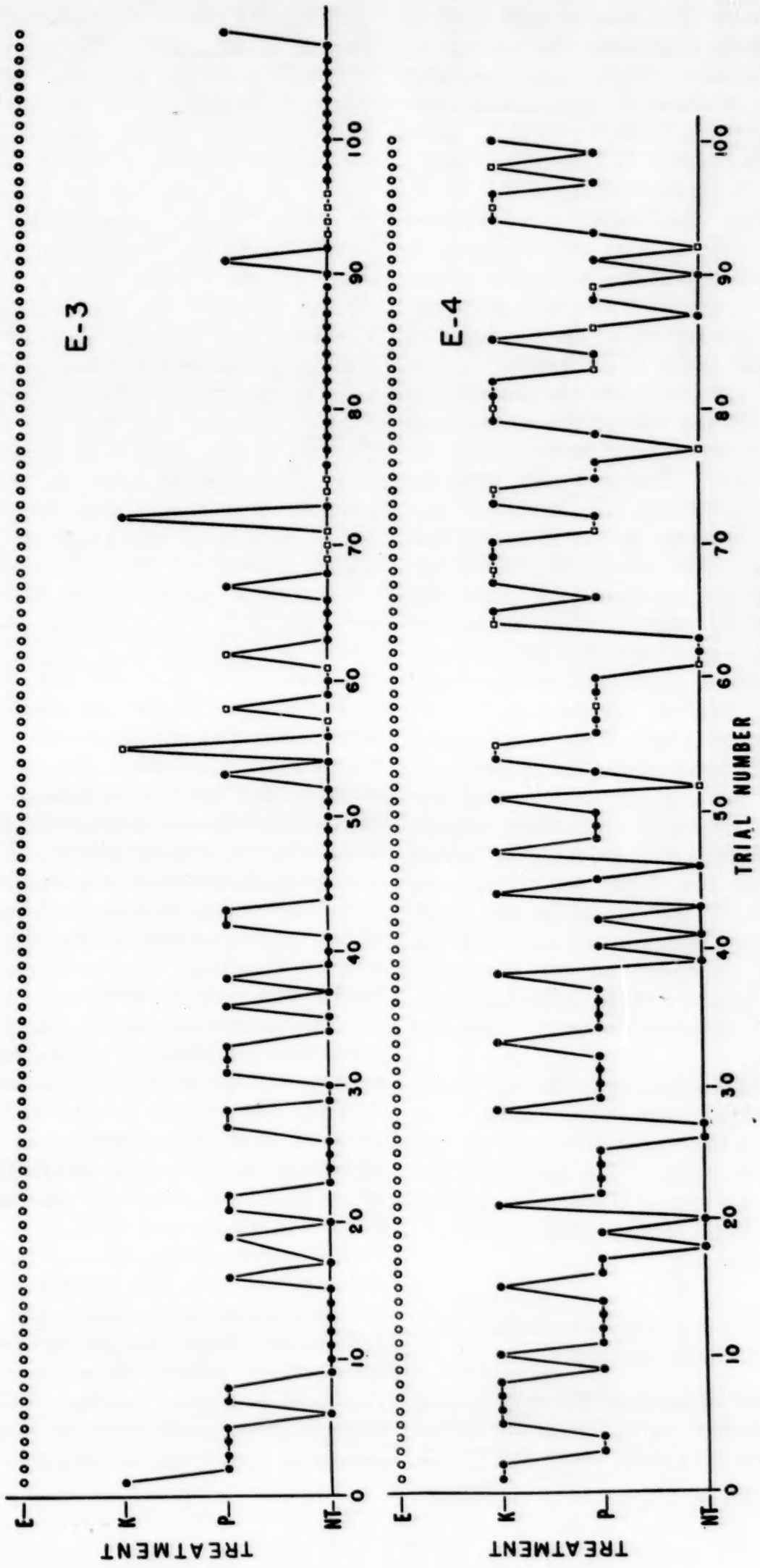

FIG. 1B. Experimental birds E–3 and E–4.

runs of more than two of each kind of butterfly were eliminated, and the following consecutive trials were possible (model or mimic = M; non-mimetic butterfly = N): (1a) M,N; (1b) M,N. (2a) N,M; (2b) N,M. (3a) M,N; (3b) N,M. (4a) N,M; (4b) M,N. Use of these randomized pairs avoided subjective repetition of any sequence in the presentation of the butterflies to the birds, and prevented the birds from reacting to the butterflies on the basis of an expected order of sequences. After each bird was given the first butterfly in a trial, it did not receive the second until each of the other birds had received its first butterfly. Thus for each bird the time interval between trial 1a and 1b was about the same as it was between trial 1b and 2a. The design of the experiments did not eliminate the possibility that the birds might predict the second butterfly given in each trial on the basis of the first one given, but the data suggested that this was not the case.

The experimental birds were given models and non-mimetic butterflies, randomly in pairs as described, until the birds had developed a relatively reliable pattern of behavior toward the model species. At this time, the mimic was substituted for the model in one trial. Subsequent substitutions of the mimic for the model depended on the particular pattern of behavior of the individual bird, and will be discussed when the data are considered.

The control birds were given mimics and non-mimetic butterflies randomly in pairs, by the same procedure used for the experimental birds. The difference between the two sets of birds was that only the experimental birds were given experience with models.

Experiments with the Monarch and Viceroy

The classic example of mimicry among North American butterflies is the Monarch-Viceroy situation, cited by Walsh and Riley (1869). In spite of a small amount of evidence to the contrary, the Monarch generally has been considered relatively unpalatable to vertebrate predators. Poulton (1909) commented upon the relative edibility of the Viceroy. He was of the opinion that the Viceroy is a Müllerian mimic, unpalatable like its model, basing his views on the supposed origin of the Viceroy from a warningly colored ancestor, like *Limenitis arthemis* (Drury), and on the assumption that warningly colored butterflies are unpalatable to predators. Walsh and Riley (1869) assumed that the Viceroy is a Batesian mimic, edible to vertebrate predators. It seemed fitting to begin the mimicry experiments with this long-debated problem of the Monarch and the Viceroy.

Geographic Distribution and Sources of Butterflies

The range of the Monarch covers North America, northeastward to central Ontario (Klots, 1951). The Viceroy is more limited in its distribution, ranging from central Canada south to South Carolina, Georgia, and Louisiana. The species possibly forms a north-south cline with *Limenitis archippus floridensis,* the mimic of the southern danaid, *Danaus gilippus berenice.* The latter mimic and model both occur in Florida. The Viceroy (*L. archippus archippus*) does not reach central Florida, which makes it certain that the Florida Scrub Jays used in these experiments had never had experience with the Viceroy in nature. However, the birds may have attempted to eat Monarchs, which are present at the Station in winter and spring.

The source of Viceroys for the feeding experiments was over-wintering hibernacula collected in Litchfield Co., Conn., in February 1956. The larvae from these were reared to the adult stage at the Archbold Biological Station. The Monarchs were obtained locally in Florida by collecting living adults and by rearing

adults from eggs obtained from females in outdoor insect cages, and also from larvae collected in the field. Both male and female butterflies were used in the experiments, but because female Viceroys resembled Monarchs more closely in size, females of this species were used in most trials. It should be noted that the relative size of models and mimics in nature is probably of little significance compared to their similarities of color and pattern, and that the effect of size on mimicry could assume a disproportionate importance under experimental conditions. The sex of a butterfly *per se* did not affect the reaction of any bird. A total of approximately 1,000 butterflies was used.

Results

The basic data for the feeding experiments with Monarchs and Viceroys are presented in figures 1A. and 1B., diagrams E–1, E–2, E–3, and E–4, and in figure 2, diagrams C–1, C–2, C–3, and C–4. The four categories of reaction to the butterflies by the birds were selected on the basis of observed behavior of the birds. "NT" means that the butterfly was not touched by the bird during the two minute test period. The NT category sometimes was accompanied by characteristic behavior on the part of a bird which will be discussed below. The "P" category means that the bird pecked the butterfly but not to the point of any injury which in nature would impair the insect's ability to reproduce. Pecking could imply tasting, but the contact of the beak of the bird with the external surface of the butterfly is what is meant here. The "K" (killed) category is used when a bird had torn the body of the butterfly so that in the wild it would have died, or could not have reproduced, but the bird left the torn specimen uneaten. "E" refers to the fact that the bird had eaten the butterfly, leaving only the wings and legs, which were picked off and discarded.

From an examination of the diagrams of the experiments (see figs. 1A and 1B;

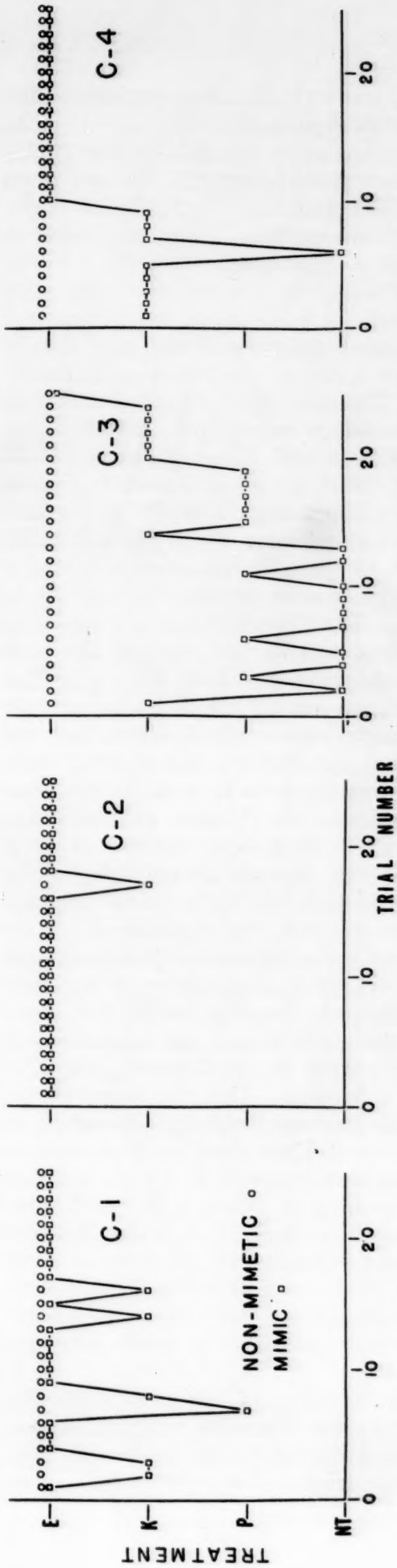

Fig. 2. Diagrams for experiments with the Monarch and the Viceroy. Control birds C–1, C–2, C–3, and C–4.

fig. 2), it will be evident that in all trials for both experimental and control birds, the non-mimetic butterfly (white circle) of each pair of butterflies in any given trial was eaten. In only four trials in this entire investigation, a bird was reluctant to eat a non-mimetic butterfly. When such hesitation occurred, the trials were stopped for a few minutes, and were not continued again until the bird readily accepted and ate the non-mimetic butterfly. Therefore every recorded trial indicates that a non-mimetic butterfly was eaten by a bird. The model, the Monarch, (black circle) was given in couplet with a non-mimetic butterfly to the four experimental birds for at least 51 trials prior to the substitution of the mimic, Viceroy, (white square) for the Monarch. The Monarch was not eaten by the four experimental birds in any trial. The diagrams for E–1, E–2, and E–3 show that during the initial trials, the Monarchs were pecked, killed, and not touched, and that the "not touched" category became more frequent as the birds learned that the Monarch was not palatable. All four birds reacted in their initial trial with the Monarch by killing or pecking the butterfly. This suggests either that the four experimental birds had not had experience with Monarchs in the field prior to capture, or, if they had experienced Monarchs in the wild, they had not remembered the unpalatability of Monarchs on sight alone under the cage conditions. That the lesson of unpalatability was never finally learned in the course of the experiments is seen in the repeated lapses of E–1, E–2, and E–3 into pecking or killing a Monarch after several trials during which the Monarch was not touched. On the basis of sight alone, E–4 was outstanding in its failure to remember for more than two successive trials that the Monarch was unpalatable.

The question of when to substitute Viceroys for Monarchs was complicated by the fact that the birds showed these periodic lapses when a model was again pecked or killed. In order to minimize the chance that a Viceroy would fall on the observed "error" pattern, i.e., the killing or pecking of the model, the presentation of each mimic was determined by the individual error pattern of each bird. A Viceroy was substituted for a Monarch soon after a bird had made an error on a Monarch. This meant that a bird had just been exposed to the unpleasant qualities of a Monarch before being offered a Viceroy. Because experience with each bird was the only guide, the technique of substitution of the mimic necessarily improved with time. For E–1, from trial 63 on, for E–2, from trial 57 on, and for E–3, from trial 63 on, no Viceroy was given unless it followed (1) a trial in which a Monarch was pecked or killed, and (2) a trial in which a Monarch was not touched, in that order. With the design of the experiments adjusted so that any pattern of natural pecking and/or killing lapses would be likely to fall on the model, as can be seen on the diagrams, the mimic was not touched.

Although E–4 did not learn to refuse the Monarch on sight, its treatment of the Viceroy shows no discrimination of the latter from the Monarch. The Viceroy was not eaten by any of the four experimental birds, and was not even killed by E–1 and E–2.

The four control birds, C–1, C–2, C–3, and C–4, were given trials with the Viceroy (mimic) and non-mimetic butterflies. Because the number of Viceroys available was limited, each control bird could be offered only 25. After these 25 Viceroys had been used, each control bird was given only the non-mimetic butterfly in each trial for the total number of trials shown in the "no. seize" column for each control bird on table 2. Each of the control birds ate every non-mimetic butterfly offered, although only the 25 which correspond to the Viceroy trials are shown in fig. 2, diagrams C–1, C–2, C–3, and C–4. The reaction to the Viceroy by C–1 indicates that it was palatable to that

TABLE 1. *Reactions of the experimental and control birds to Viceroys*

A. Comparison of no. "not touched" *vs.* no. "pecked—killed—eaten"

	Control birds				Experimental birds			
	C-1	C-2	C-3	C-4	E-1	E-2	E-3	E-4
NT	0	0	9	1	14	12	12	4
P—K—E	25	25	16	24	2	1	3	12

B. Comparison of no. "not touched—pecked—killed" *vs.* no. "eaten"

	Control birds				Experimental birds			
	C-1	C-2	C-3	C-4	E-1	E-2	E-3	E-4
NT—P—K	6	1	24	9	16	13	15	16
E	19	24	1	16	0	0	0	0

bird in most of the trials (diagram for C–1). C–2 ate the Viceroy in all but one trial as the diagram shows. In the case of C–3, most of the Viceroys were not touched, or were pecked or killed, and in only one trial, the last, was a Viceroy eaten. In the first nine trials, C–4 killed Viceroys, and once did not touch a Viceroy, but from trial 10 on, it ate all Viceroys.

STATISTICAL ANALYSIS OF THE DATA

Table 1,A shows a comparison of the treatment of the Viceroy for the category "NT" compared with the lumped categories "P-K-E" for all eight birds. On the hypothesis that the experimental birds and the control birds reacted to the Viceroy in the same way, a chi-squared test gave a value of 80.81, d.f. = 7, with the Yates correction factor, which was used in all chi-squared tests (table 1,A). The probability of obtaining these results, or worse ones, given this hypothesis, is less than .001. It may therefore be said that the two groups of birds did not react to the Viceroy in the same way, and that the control birds pecked, killed, and ate Viceroys significantly more than the experimental birds did. Similarly, when the data were analyzed to compare the categories "NT-P-K" with "E," the chi-squared value was 116.81, d.f. =7, P less than .001 (table 1,B). The control birds ate significantly more Viceroys than the experimental birds did; in fact, no Viceroys were eaten by the latter group.

In addition to an analysis of the response to the Viceroys by the experimental and control bird groups, con-

TABLE 2. *Reaction times of jays in seizing butterflies (in seconds to the nearest whole second)*

	Monarch					Viceroy					Non-mimetic butterflies				
Birds	Mean time seize	Min. time	Max. time	No. seize	No. NT	Mean time seize	Min. time	Max. time	No. seize	No. NT	Mean time seize	Min. time	Max. time	No. seize	No. NT
C-1	—	—	—	—	—	8	1	100	25	0	3	1	14	92	0
C-2	—	—	—	—	—	5	2	11	25	0	5	2	25	95	0
C-3	—	—	—	—	—	10	1	36	16	9	1	1	3	101	0
C-4	—	—	—	—	—	11	2	46	24	1	6	1	76	94	0
E-1	9	1	31	12	76	14	6	22	2	14	1	1	3	102	0
E-2	27	1	102	25	48	20	20	20	1	12	1	1	2	84	0
E-3	36	1	119	24	69	22	4	41	3	12	2	1	16	108	0
E-4	12	1	88	72	12	30	2	112	12	4	3	1	10	100	0

sideration was also given to the reaction times of the birds in seizing the butterflies. The measure of time which has particular application for mimicry is the interval between the time a bird first saw a butterfly placed in its cage to the time when the bird first pecked or seized the butterfly. The mean time in seconds that each bird took to seize the Monarch, the Viceroy, and the non-mimetic butterflies used in the present experiments was calculated, and is shown on table 2. To indicate the range of seconds for each bird in seizing the butterflies of each group, the minimum and maximum times in seconds are also given. Since the experimental birds did not touch many Monarchs and Viceroys, the number of butterflies seized (from which the means were calculated) and also the number that were not touched are given in separate columns.

As table 2 shows, the time which the experimental birds took to seize Monarchs and Viceroys was considerably greater than that for non-mimetic butterflies, which suggests that the birds did not discriminate the Viceroy from the Monarch. If a similar hesitation in seizing a Monarch and its mimic were shown by an experienced bird in nature, escape of the butterfly from predation would be likely because of the time factor alone.

These data also suggest a correlation with the relative palatability of the various butterflies. The mean-times-seize of all the birds for the palatable non-mimetic butterflies are less than those of the control birds for the Viceroy.

Behavior of the Scrub Jays

In the description of the categories of reaction to the butterflies by the birds, it was noted that the "NT" category was sometimes accompanied by characteristic behavior on the part of a bird. This consisted of the bird ruffling its feathers and shaking its body, and/or by what I termed a "hop routine." The hop routine was a repetition of a series of hop movements by a bird, from perch, to side of cage, to floor, to perch, which often persisted for the full two minutes of a test, if an unpalatable model or its mimic had been presented.

A detailed examination of the occurrence of the feather-ruffling reaction in the individual birds shows a definite correlation between the reaction and the unacceptability of a given butterfly species to a bird. For the experimental birds, the feather-ruffling often occurred when either a Monarch or a Viceroy was presented. Thus E–1 gave this reaction in 77 out of 88 trials (88%) with the Monarch, and in 13 out of 16 trials (81%) with the Viceroy. The reaction was given by E–2 in 43 out of 73 trials (59%) with the Monarch, and in 9 out of 13 trials (69%) with the Viceroy. E–3 gave the reaction in 42 out of 94 trials (45%) with the Monarch, and in 5 out of 15 trials (33%) with the Viceroy. E–4 showed this reaction in 6 out of 84 trials (7%) with the Monarch, and in 2 out of 16 trials (13%) with the Viceroy. The reaction was never given by any of the birds when a non-mimetic butterfly (palatable) was presented.

The control birds also gave this same reaction when the Viceroy was presented, although on the whole less frequently than the experimental birds did. C–1 gave the reaction for 3 out of 25 Viceroys (12%); C–2 for 0 out of 25 Viceroys (0%); C–3 for 19 out of 25 Viceroys (76%); C–4 for 3 out of 25 Viceroys (12%). As might have been expected on the basis of the experimental birds, C–3, the bird that reacted to the Viceroy as an unpalatable butterfly during all but the last trial, also gave a high proportion of feather-ruffling reactions to the Viceroy.

Learning and Memory in the Scrub Jays

Although a study of learning in the Florida Scrub Jays was not the primary purpose of this inquiry, a few words

should be devoted to this aspect of the experiments. De Ruiter (1952) described, in his work with Jays (*Garrulus glandarius* Linné) and Chaffinches (*Fringilla coelebs* Linné), how the birds became used to the inedibility of small sticks, and refused to peck at them. After experience with the twigs, the birds also refused to peck at caterpillars bearing close similarity to the twigs. Only if a caterpillar were pecked by accident would the birds, thus rewarded, continue to hunt for caterpillars. If they found only sticks again, they soon ceased pecking. This behavior has been termed an example of habituation by Thorpe (1956). In so far as the Scrub Jays found the Monarch butterfly inedible in a series of 50 trials, one might have expected habituation to develop in the course of the experiments. Indeed, the theory of mimicry suggested by Müller (1879, 1881) assumes that young birds learn by experience which butterflies are inedible and remember what they have learned. However, the repeated lapses of the Scrub Jays into pecking the Monarch show a persistent trial-and-error learning pattern. Swynnerton (1915) in referring to the mistaken attacks of his caged birds on unpalatable insects noted: ". . . no bird could be too old or too experienced to make continual mistakes of this kind." Similar "forgetfulness" is reported by Sadovnikova (1923). She found that in maze learning in passerine birds, individual birds would occasionally show periods of "forgetting" when they entered blind alleys which they had previously learned to avoid. The pattern of apparent forgetfulness shown by the Scrub Jays thus may be of a general nature, or may be associated with cage experiments. The experimental behavior can not be extended to imply that such short-term forgetfulness (day to day) exists among Scrub Jays in the wild; this is not known.

In spite of the short-term lapses of memory seen in the Scrub Jays, the data did show that the birds could remember to reject a Monarch and a Viceroy on sight alone after a period of about two weeks. E–1 rejected a Monarch and a Viceroy after 16 days of 82 trials with unrelated butterflies of the *Battus* mimicry complex; E–2, after 19 days of 84 such interim trials; E–3, after 15 days of 82 such interim trials. Tests of memory in the Scrub Jays after longer periods had elapsed were not possible in these experiments.

Discussion

The first point to be considered is that of the reaction to the model, the Monarch, by the four experimental birds. As the data showed, the Monarch was unacceptable on sight alone at some time to all the experimental birds. The theory that models are unpalatable, and that their color pattern is a sign of unpalatability, is thus supported. Following a period of learning during which the experimental birds were given the Monarch, these birds did not even touch the Viceroy in many trials, and in no case did the birds eat a Viceroy. That the Viceroy is not as inherently unpalatable as the Monarch was shown by the control birds, and this will be discussed below. The highly significant difference in the treatment of the Viceroy by the two sets of birds is attributed to the experience of the experimental birds with the unpalatable Monarch, and to the subsequent association by these birds of the color pattern of the Viceroy with that of the Monarch. Under the conditions of the experiment, it has been shown that mimicry in the case of the Monarch and Viceroy is effective.

The status of the edibility of the Viceroy demands further consideration. According to Bates's idea (1862), the mimic was presumed to be a butterfly edible to vertebrate predators, especially to birds. Müller (1879), in dealing with a particular complex of closely related species of mimetic butterflies in South America (Heliconiidae) which had puzzled Bates, resolved the problem by suggesting that

the entire complex of "models" and "mimics" was unpalatable to predators. The pooling of their numbers thus reduced the number of losses per species to the learning of inexperienced birds. In the present experiments, the status of the Viceroy as a Batesian or Müllerian mimic is not entirely evident, and it brings to mind Swynnerton's repeated emphasis on the range of edibility of butterflies to birds (1919). That the experimental birds in no instance regarded the Viceroys as edible is clear. The reaction to the Viceroy by E–1 and E–2 (fig. 1A) shows that those birds never killed that butterfly, although E–2 killed three Monarchs after the commencement of Viceroy trials. E–1 and E–2 were not discriminating the Viceroy from the Monarch as something different and edible. E–3 (fig. 1B) in trial 55 apparently did discriminate between its first Viceroy and Monarchs. Subsequent trials indicate either that the bird failed to maintain its discriminative ability, perhaps in part due to the design of the trials plus the adjustment for natural error, or that the bird found the Viceroy unpalatable, and established a general reaction to both Monarch and Viceroy as inedible. The fluctuating responses of E–4 (fig. 1B) to the Monarch and Viceroy show that the bird failed to remember on sight alone that the Monarch was inedible. The treatment of the Monarch and Viceroy was so consistent that it seems likely that this bird was not discriminating between the two, and perhaps found them both unpalatable. At any rate the Viceroy was not eaten in preference to the Monarch by E–4.

All four experimental birds showed identical, characteristic behavior, discussed above, to both the Monarch and Viceroy, which supports the idea that there was no discrimination of one from another. However, although the Monarch and Viceroy were treated in this generalized manner, a trial can be cited in which a bird clearly distinguished one Viceroy from Monarchs on the basis of a slight difference in color. For E–3, trial 62, there is reason to believe that the pecking of this Viceroy was due to its coloration which was somewhat more brown than previous or succeeding ones. The butterfly had been presented inadvertently, and the instant curiosity and pecking reaction of the bird to the slight color discrepancy was noted. The problem of discrimination *vs.* generalization of models and mimics by the Scrub Jays will be discussed in more detail in Part III of this series of papers. For the present, it can be said that although the data for the experimental birds show that the Viceroy was rejected by them, they do not clearly show why. For E–1 and E–2, the rejection of the Viceroy seems to be based on the fact that the birds learned that the Monarch was unpalatable, and could not discriminate the Viceroy from the Monarch. The data for E–3 and E–4 could be interpreted in the same way as for E–1 and E–2, or alternatively, that the Monarch and Viceroy were both found by experience to be unpalatable and were recognized as one or as separate color patterns, but in either case rejected.

The control birds gave further indication of the inherent edibility of the Viceroy. As the diagrams showed (fig. 2), the Viceroy was not as edible as the non-mimetic butterflies for C–3, and in part this was true for C–1 and C–4. C–2 regarded the Viceroy as an edible species. C–4 appears to have learned to eat the Viceroy. The reaction of C–3 to the Viceroy is comparable to the initial learning pattern of E–1 for the Monarch, but the Viceroy was more acceptable to C–3 toward the end of the experiment. It is possible that the control birds, particularly C–3, had some pre-capture experience with the Monarch, and associated the Viceroy with the Monarch, although no bird refused to peck its first Viceroy. The geographic distribution of the Viceroy precludes any experience with that exact color pattern in nature by these jays.

The learning patterns of E–3 and E–4 and of C–1, C–3, and C–4 could be interpreted to lend support to the hypothesis that the Viceroy is a classical Müllerian mimic. Additional evidence for this view is suggested by the reaction times of the control birds in seizing Viceroys, which were longer than those for seizing non-mimetic butterflies. However, rather than try to place the Viceroy in a rigid, all-or-none category which implies more than the data show, the Viceroy is here considered more edible than its model, the Monarch, but initially less edible (except to C–2) than the non-mimetic butterflies used in these experiments.

Summary

1) This paper is the first in a series of three which present experimental studies of mimicry in some North American butterflies.

2) The experiments were designed to study the effectiveness of mimicry in these butterflies with the use of eight Florida Scrub Jays (*Cyanocitta coerulescens coerulescens*) as caged predators. The butterflies were immobilized and their wings were folded together dorsally, so that only mimicry in the characters of the underside of the wings was being tested in these experiments.

3) The present experiments tested mimicry in the classic example of the Monarch (*Danaus plexippus*) and Viceroy (*Limenitis archippus archippus*).

4) The results of these experiments show that the non-mimetic butterflies, used in couplet with each model or mimic, were eaten in every trial by all birds.

5) The four experimental birds were given numerous trials with the model, the Monarch. The Monarch was not eaten by these birds in any trial, and in many trials was not touched, after initial learning had taken place.

6) After the experimental birds had been given more than 50 trials with the Monarch, the Viceroy was substituted for the Monarch at intervals. The Viceroy was never eaten by the four experimental birds, and in many trials was not even touched.

7) Characteristic behavior shown by the four experimental birds after the presentation of both Monarchs and Viceroys indicated no discrimination between the two species of butterflies.

8) The four control birds had no prior laboratory experience with the Monarch, and these birds ate the Viceroy in many trials.

9) A statistical analysis of the reaction to the Viceroy by the experimental and control birds indicated that the two groups did not react to the Viceroy in the same way. The difference in response is attributed to the prior laboratory experience of the experimental birds with the Monarch. The color pattern of the Viceroy was apparently associated with the complete inedibility and similar color pattern of the Monarch. Under the conditions of the experiment, mimicry has been shown to be effective.

10) The data indicate that the Viceroy is more edible than the Monarch, but less edible than the non-mimetic butterflies used in the experiments. In addition, the control birds took longer to seize Viceroys, on the average, than they took to seize the non-mimetic butterflies. Therefore the Viceroy is not termed either a Batesian or a Müllerian mimic in the classical sense.

11) Learning behavior and memory in the Scrub Jays were considered briefly. The records showed that three of the four experimental birds remembered to reject a Monarch and a Viceroy on sight alone, after a period of over two weeks had elapsed since their last experience with these butterflies.

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THE NIGER, THE VOLTA AND THE DAHOMEY GAP AS GEOGRAPHIC BARRIERS

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The most concise summary of zoogeographic data on West African mammals at present extant is that of Dekeyser (1955). With regard to the forested part of this region, he concludes briefly that "there is a block (the Guinea Forest Block) . . . stretching from French Guinea to Togo; a peculiar stretch, the Dahomey Gap, which can be defined as a forest relic, comprising 'islands and galleries' which are inter-connected, at least in the rainy season. With the outlying forests of (Western) Nigeria, the easterly Congo Forest Block commences . . . we shall see below that some species are distributed throughout the High Forest zone, while others are restricted either to the Guinea (western) Forest Block or to the Congo Forest Block."

In its present (and very recent past) condition, the Guinea Forest Block stretches as a solid continuum of varying depth from the Volta westward to Sierra Leone and southeastern French Guinea. The Congo Forest Block stretches approximately from the Wemé River, near the western border of Nigeria, to the Rift Valley, on the eastern border of the Belgian Congo. The area between the Volta and the Wemé is an area of mixed High Forest, Guinea Savannah and Coastal Scrub and Grassland (terms as used in Taylor, 1952). The High Forest is most abundant in Western Togoland ("British Togoland"), and becomes less so in Eastern Togoland and Dahomey, but nowhere is it the solid, continuous mass that we find in the Guinea Forest Block and the Congo Forest Block.

It is therefore appropriate to consider the Dahomey Gap at present to be bounded by the Volta on the west and the Wemé on the east (fig. 1). This is not the precise delimitation given by Dekeyser in his text, but is clearly intended in his map (1955, p. 77).

In an earlier paper (Booth, 1954), the extant data on the distribution of High Forest mammalian subgenera in West Africa was summarized. It was concluded that the Dahomey Gap was probably of considerable and long-standing importance. Aubréville (1949a) had already indicated that it was the first area likely to be drastically affected by climatic deterioration (desiccation). Zoogeographic data also seemed to show that there had been at some stage complete isolation of the Guinea Forest Block from the Congo Forest Block, permitting of independent evolution on either side of the Dahomey Gap. There was further a suggestion that at certain periods the Dahomey Gap had been much wider than it is at present, and that this was responsible for the paucity of mammalian subgenera found in Western Nigeria. All the subgenera which occur in Western Nigeria (west of the Niger) are also to be found in both the Gold Coast and Eastern Nigeria, with the one exception of *Stochomys*. (*Hydrictis*, previously thought endemic to the Congo Forest Block, proves to be present both in the Gold Coast, and, T. S. Jones informs me, in Sierra Leone.)

The present contribution will examine the situation more closely, in terms of well-known and conspicuous mammals, and of lower taxonomic categories. It will also deal with an area considered to be within the Dahomey Gap itself.

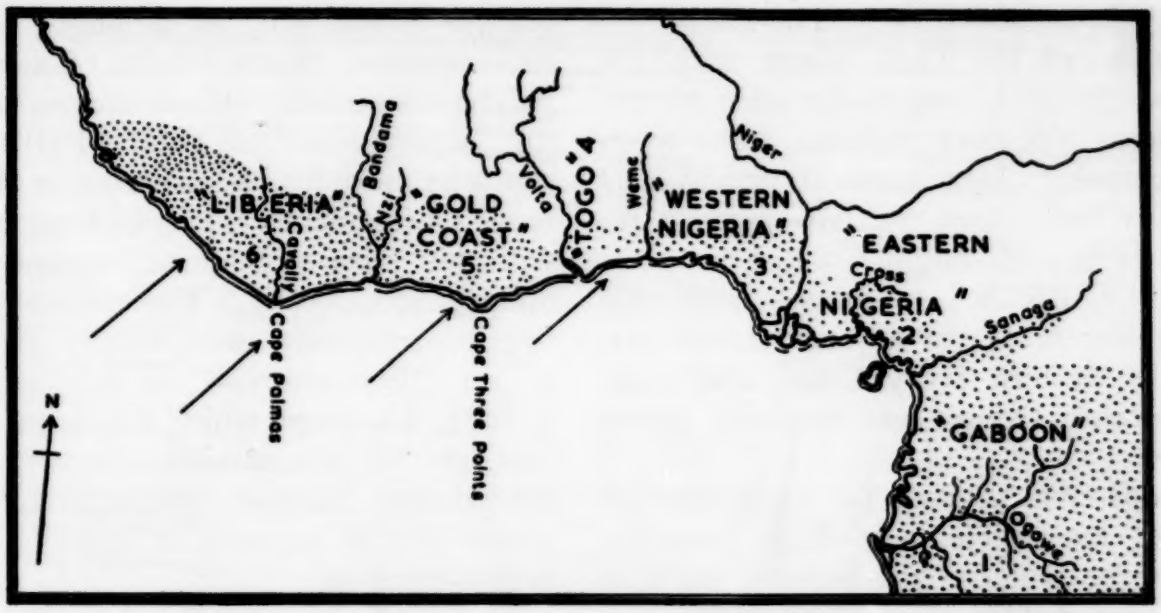

FIG. 1. Map of West Africa, the High Forest zone (stippled) being divided into the 6 regions as in the text. The arrows show the direction of the rain-bearing southwest monsoon.

PROCEDURE

The analysis is divided into two distinct parts:

1. The distribution of Primates, Sciuromorpha, Artiodactyla and Hyracoidea in High Forest from Gaboon to Sierra Leone, the unit being the "species-group."

2. The distribution of these mammals by species and subspecies between the Volta and the Niger.

57 species-groups are considered. The following are omitted, as being definitely amphibious and generally associated with rivers: *Hippopotamus, Choeropsis, Hyemoschus, Limnotragus. Epixerus,* clearly a recent arrival in the High Forest zone, is also omitted. The main sources of the data are: Baudenon (1952), Booth (1956b, c), Cansdale (1948), Dekeyser (1955), Malbrant & Maclatchy (1949) and Rosevear (1952).

The area has been divided further than in the earlier paper. The divisions are as follows (fig. 1).

1. "GABOON." This region is included primarily because it gives a picture of the situation in the richer parts of the Congo Forest Block. It includes the territories of Gaboon, Spanish Guinea and the Cameroons south of the Sanaga River. In terms of physical geography, it comprises the basins of all those river systems which run into the Atlantic between the Congo and the Sanaga.

2. "EASTERN NIGERIA." This region includes the High Forest zone between the Sanaga and the Niger. As Rosevear (1953) has pointed out, the Cross River is in many instances an apparently important barrier preventing the Cameroons fauna from reaching the Niger. Rosevear also remarks, however, that there has been no systematic exploration of the area between the Cross and the Niger. The tendency has been to regard the Cross as the western boundary of the "Cameroons," a much-explored and over-glamourised region; consequently it is possible that too much stress has been laid on its importance, on insufficient grounds.

3. "WESTERN NIGERIA." This is a small region, stretching from the Niger to the Wemé. It represents the western tip of Dekeyser's Congo Forest Block.

4. "TOGOLAND." The forested area of Togoland is here included, together with that part of the old political territory of the Gold Coast which lay east of the Volta. The region lies within the Dahomey Gap, of which it constitutes the western half.

5. "GOLD COAST." The High Forest zone of the Gold Coast with the eastern Ivory Coast as far west as the Bandama-Nzi river system. (The western boundary here given is provisional: a fuller account of the two western regions is in preparation.)

6. "LIBERIA." Liberia, with the High Forest of the adjacent territories, namely western Ivory Coast, southeastern French Guinea and southern Sierra Leone.

Unfortunately, data for Dahomey are as yet incomplete. In those instances where the fauna of the forested parts of Togoland differs from that of Western Nigeria, it would be most interesting to have an exact indication of the nature of the boundary concerned.

Before proceeding further, it is necessary to explain the choice of the "species-group" as the unit of analysis in the first half of this paper. Some of these species-groups consist only of a single, monotypic species. Some consist of a single, polytypic species. Others correspond to the "superspecies" of Mayr (1931), and comprise more than one species, or "hemispecies," the members of which generally, with but rare exceptions, replace each other geographically. The species-group, then, corresponds most closely perhaps to the "Formenkreis" of Kleinschmidt (1900), a concept which has been much criticized by taxonomists, but which is, nevertheless, almost instinctively employed by the majority of ecologists and field naturalists.

The species-groups listed in Table 1, which shows the distribution of group, correspond exactly to the 'species' of G. M. Allen (1939) except in the following cases:

1. *Cercopithecus petaurista* and *C. nictitans* are regarded as entirely separate. Sanderson (1940) was severely criticised by Schwarz

TABLE 1. *Distribution of species groups*

	1 Gaboon	2 E. Nigeria	3 W. Nigeria	4 Togo	5 Gold Coast	6 Liberia	Category
Primates							
Arctocebus calabarensis	+	+	−	−	−	−	C
Perodicticus potto	+	+	+	+	+	+	A
Galago alleni	+	+	−	−	−	−	C
Galagoides demidovii	+	+	+	+	+	+	A
Euoticus elegantulus	+	+	−	−	−	−	C
Cercopithecus mona	+	+	+	+	+	+	A
Cercopithecus petaurista	−(+)	−	+	+	+	+	B
Cercopithecus cephus	+	+	+	−	−	−	C
Cercopithecus nictitans	+	+	+	−	−	+	B
Cercopithecus neglectus	+	−	−	−	−	−	C
Cercopithecus diana	−(+)	−	−	−	+	+	B
Cercopithecus l'hoesti	−(+)	+	−	−	−	−	C
Miopithecus talapoin	+	−	−	−	−	−	C
Cercocebus torquatus	+	+	−	−	+	+	B
Cercocebus galeritus	+	−	−	−	−	−	C
Cercocebus albigena	+	−	−	−	−	−	C
Papio leucophaeus	+	+	−	−	−	−	C
Papio sphinx	+	−	−	−	−	−	C
Colobus polykomos	+	+	+	+	+	+	A
Procolobus verus	−	−	−	+	+	+	D
Procolobus badius	−(+)	+	−	−	+	+	B
Pan troglodytes	+	+	+	−	+	+	B
Gorilla gorilla	+	+	−	−	−	−	C
	18(+4)	15	8	6	10	11	

TABLE 1—*Continued*

	1 Gaboon	2 E. Nigeria	3 W. Nigeria	4 Togo	5 Gold Coast	6 Liberia	Category
Sciuromorpha							
Anomalurus peli	−	−	−	−	+	+	D
Anomalurus derbianus	+	+	+	−	+	+	B
Anomalurus pusillus	+	−	−	−	−	−	C
Anomalurops beecrofti	+	+	+	+	+	+	A
Idiurus zenkeri	+	+	−	−	+	+	B
Zenkerella insignis	+	−	−	−	−	−	C
Funisciurus auriculatus	+	+	+	+	−	−	C
Funisciurus pyrrhopus	+	+	+	+	+	+	A
Funisciurus lemniscatus	+	+	−	−	−	−	C
Funisciurus mystax	+	−	−	−	−	−	C
Heliosciurus gambianus	+	+	+	+	+	+	A
Heliosciurus cooperi	−	+	−	−	−	−	C
Heliosciurus poensis	+	+	−	−	+	+	B
Myosciurus pumilio	+	+	−	−	−	−	C
Protoxerus stangeri	+	+	+	+	+	+	A
Protoxerus aubinni	−	−	−	−	+	+	D
Epixerus wilsoni	+	−	−	−	+	+	B
	14	11	6	5	10	10	
Artiodactyla							
Potamochoerus porcus	+	+	+	+	+	+	A
Hylochoerus meinertzhageni	+	−	−	−	+	+	B
Tragelaphus scriptus	+	+	+	+	+	+	A
Taurotragus eurycerus	+	−	−	+	+	+	B
Syncerus nanus	+	+	+	+	+	+	A
Cephalophus zebra	−	−	−	−	−	+	D
Cephalophus dorsalis	+	+	−	−	+	+	B
Cephalophus ogilbyi	+	+	−	+	+	+	B
Cephalophus niger	−	−	+	+	+	+	D
Cephalophus nigrifrons	+	−	−	−	−	−	C
Cephalophus callipygus	+	−	−	−	−	−	C
Cephalophus silvicultor	+	+	+	+	+	+	A
Cephalophus jentinki	−	−	−	−	−	+	D
Cephalophus monticola	+	+	+	+	+	+	A
Neotragus pygmaeus	−	−	−	−	+	+	D
Hylarnus batesi	+	+	−	−	−	−	C
	12	8	6	8	11	13	
Hyracoidea							
Dendrohyrax dorsalis	+	+	+	−	+	+	B
	1	1	1	−	1	1	
Totals	45(+4)	35	21	19	32	35	

(1954) for this opinion, but Booth (1956a) has shown that it was entirely justified. Separated under the *petaurista*-group are three species: *C. petaurista* (including *C. p. büttikoferi*), *C. erythrogaster* and *C. ascanius* subspp. of Schouteden (1947).

2. *Procolobus badius* and *P. verus* are very distinct species, as shown by Hill (1952), and are placed in separate groups.

3. All "species" of *Idiurus* are placed in the *I. zenkeri*-group.

4. The group *Funisciurus pyrrhopus* includes

F. pyrrhopus subspp., *F. leucostigma* subspp., *F. anerythrus* subspp., *F. substriatus*, *F. mandingo* subspp., and *F. raptorum*.

5. The *Heliosciurus gambianus*-group corresponds to the "species" of Ingoldby (1927). Since Ingoldby's taxonomic procedure received such unfortunately wide acclaim, it has been difficult to disentangle this group.

6. The *Heliosciurus cooperi*-group is erected for that very distinct species alone, described since the publication of Allen's checklist.

7. The *Epixerus ebii*-group comprises the genus *Epixerus*.

8. The *Cephalophus ogilbyi*-group comprises the subgenus *Cephalopia* Knottnerus-Meyer, and includes *C. leucogaster*.

9. The *Cephalophus monticola*-group comprises the subgenus *Philantomba* (= *Guevei*).

Analysis

The same four categories are distinguished as in the earlier paper, namely:

A. Groups with *overall* distribution. Those groups which are represented in all six regions.

B. Groups with *general* distribution. Those groups which, though widespread, are absent from one or more regions. They are invariably present in region 6 and in region 1 or 2, or in the Congo basin.

C. *Endemic central* groups. Groups which are absent from regions 5 and 6.

D. *Endemic western* groups. Groups which are absent from regions 1 and 2.

Fifty-seven groups are recognized. They fall into the four categories as follows:

A. Overall. 13 groups.
- Primates: *Perodicticus potto, Galagoides demidovii, Cercopithecus mona, Colobus polykomos.*
- Sciuromorpha: *Anomalurops beecrofti, Funisciurus pyrrhopus, Heliosciurus gambianus, Protoxerus stangeri.*
- Artiodactyla: *Potamochoerus porcus, Tragelaphus scriptus, Syncerus nanus, Cephalophus silvicultor, C. monticola.*

B. General. 15 groups.
- Primates: *Cercopithecus petaurista, C. nictitans, C. diana, Cercocebus torquatus, Procolobus badius, Pan troglodytes.*
- Sciuromorpha: *Anomalurus derbianus, Idiurus zenkeri, Heliosciurus poensis, Epixerus ebii.*
- Artiodactyla: *Hylochoerus meinertzhageni, Taurotragus eurycerus, Cephalophus dorsalis, C. ogilbyi.*
- Hyracoidea: *Dendrohyrax dorsalis.*

C. Endemic Central. 22 groups.
- Primates: *Arctocebus calabarensis, Galago alleni, Euoticus elegantulus, Cercopithecus cephus, C. neglectus, C. l'hoesti, Miopithecus talapoin, Cercocebus galeritus, C. albigena, Papio leucophaeus, P. sphinx, Gorilla gorilla.*
- Sciuromorpha: *Anomalurus pusillus, Zenkerella insignis, Funisciurus auriculatus, F. lemniscatus, F. mystax, Heliosciurus cooperi, Myosciurus pumilio.*
- Artiodactyla: *Cephalophus nigrifrons, C. callipygus, Hylarnus batesi.*

D. Endemic Western. 7 groups.
- Primates: *Procolobus verus.*
- Sciuromorpha: *Anomalurus peli, Protoxerus aubinni.*
- Artiodactyla: *Cephalophus zebra, C. niger, C. jentinki, Neotragus pygmaeus.*

The composition of the fauna of the six regions is as follows:

Region 1. "GABOON": 45 groups. −13 overall; 12 general (includes all general groups except the 3 Primates *Cercopithecus petaurista, C. diana, Procolobus badius*); 20 endemic central (includes all endemic central groups except *Cercopithecus l'hoesti* and *Heliosciurus cooperi*). The 4 Primates which are mentioned above as absent from Gaboon are represented in the Congo Basin, and are marked (+) for Region 1 in table 1, but not counted in the totals. *Heliosciurus cooperi* appears to be unique to Region 2.

Region 2. "EASTERN NIGERIA": 35 groups. −13 overall; 10 general (includes all general groups except *Cercopithecus petaurista, C. diana, Epixerus ebii, Hylochoerus meinertzhageni, Taurotragus eurycerus*); 12 endemic central

(*Arctocebus calabarensis, Galago alleni, Euoticus elegantulus, Cercopithecus cephus, C. l'hoesti, Papio leucophaeus, Gorilla gorilla, Funisciurus auriculatus, F. lemniscatus, Heliosciurus cooperi, Myosciurus pumilio, Hylarnus batesi*).

Region 3. "WESTERN NIGERIA": 21 groups. −13 overall; 5 general (*Cercopithecus petaurista, C. nictitans, Pan troglodytes, Anomalurus derbianus, Dendrohyrax dorsalis*); 2 endemic central (*Cercopithecus cephus, Funisciurus auriculatus*); 1 endemic western (*Cephalophus niger*).

Region 4. "TOGOLAND": 19 groups. −13 overall; 3 general (*Cercopithecus petaurista, Taurotragus eurycerus, Cephalophus ogilbyi*); 1 endemic central (*Funisciurus auriculatus*); 2 endemic western (*Procolobus verus, Cephalophus niger*).

Region 5. "GOLD COAST": 32 groups. −13 overall; 14 general (includes all general groups except *Cercopithecus nictitans*); 5 endemic western (includes all endemic western groups except *Cephalophus zebra* and *C. jentinki*).

Region 6. "LIBERIA": 35 groups. −13 overall; 15 general; 7 endemic western.

Comparing regions 1 and 6, those regions within the area under consideration which are furthest away from the Dahomey Gap, we find that region 1, "Gaboon," is far richer; by definition this richness consists in a greater number of endemic groups. At the same time, 25 of the 35 groups found in "Liberia" are also represented in "Gaboon." It is therefore a reasonable supposition (and indeed has always been held to be so) that the fauna of the Guinea Forest Block of Dekeyser is derived originally from that of the Congo Forest Block, but that a number of groups failed to penetrate West Africa at all. On the other hand, the differentiation of groups now restricted to "Liberia" or to "Liberia" and "Gold Coast" indicates that there has to some degree been independent evolution of the faunas of the Congo and Guinea Forest Blocks.

If we now compare regions 2 and 5, the regions next in position, nearer the Dahomey Gap, we find that their faunas are in terms of species groups nearly equally rich, that of region 2, "Eastern Nigeria," being only slightly the richer. That of region 5 "Gold Coast," is simpler. It can be said to be derived entirely from that of region 6, with three groups missing. Two of these groups, *Cephalophus zebra* and *C. jentinki,* are now endemic to region 6, one is a general group. The endemics permit of the simple explanation that they may have evolved and remained in region 6. As is the case with the endemics of region 1, however, this is not the only possible explanation. They may have evolved elsewhere, and become secondarily restricted to their present geographic range. The general group absent from "Gold Coast" is *Cercopithecus nictitans.* Since it occurs in "Western Nigeria," and since at this level parallel evolution is most unlikely to have been significant, the group must formerly have been present in "Gold Coast" also. Region 2 presents a more complex picture than region 5. The fauna largely resembles that of region 1, but one endemic group appears in the Cameroons Highlands, namely *Heliosciurus cooperi.* Moreover, two monkeys, *Cercopithecus l'hoesti* and *Procolobus badius,* though represented in "Eastern Nigeria" and in the Congo Basin, are absent from "Gaboon."

While, therefore, there can be no objection to the statement that the "Gold Coast" fauna may actually have been supplied at a rather late date from "Liberia" we cannot assert that the "Eastern Nigeria" fauna has similarly been supplied entirely from that of "Gaboon," though it may largely have been.

In regions 3 and 4 we find the forest fauna reduced to a comparatively small number of species-groups. Both regions (figs. 2 and 3) are not only about one third poorer than any other region, but

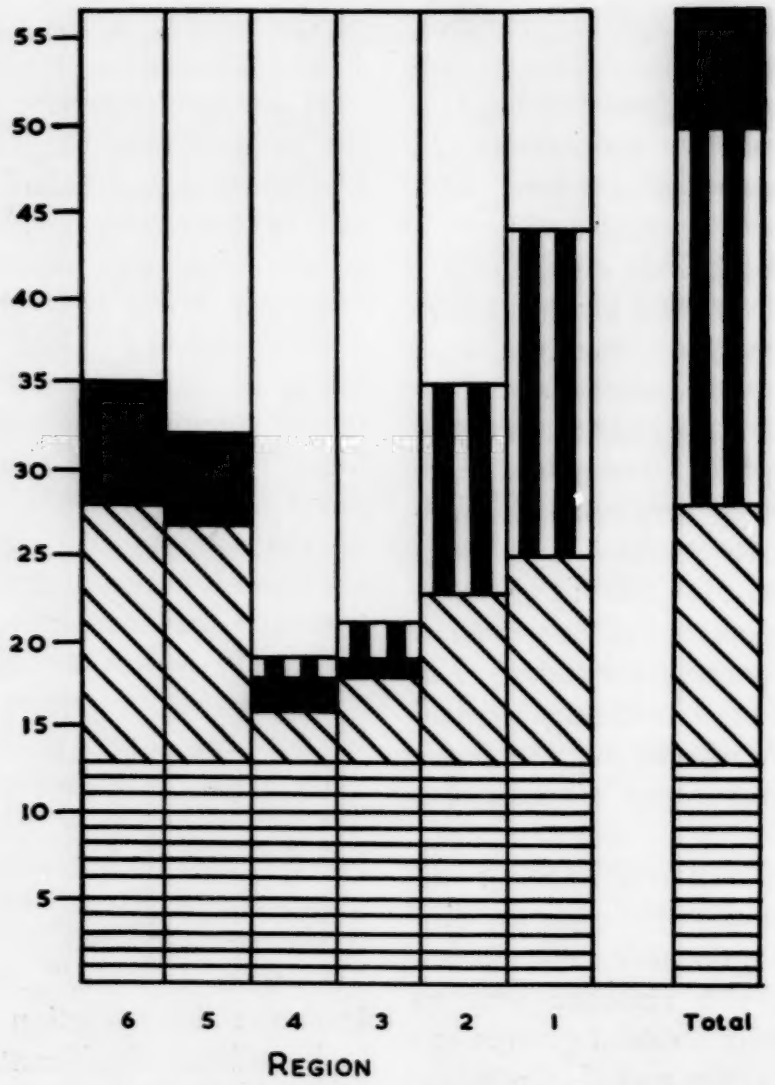

FIG. 2. The numbers of species-groups occurring in the 6 regions. Horizontal shading—overall groups; diagonal shading—general groups; vertical stripes— endemic central groups; solid black—endemic western groups.

also contain between 60% and 70% of overall groups. The degree of ecological tolerance shown by the various groups inhabiting regions 3 and 4 is of some interest. All the overall groups are ecologically highly tolerant. All can be found in the Gold Coast and Togoland well to the north of the High Forest zone proper, in the riparian forests of the Volta and Oti Rivers, from which environment many other High Forest mammals are absent. *Tragelaphus scriptus* and *Syncerus nanus,* as well as the nominate form of *Heliosciurus gambianus,* are found in the savannah itself. Of the other groups found in the forests of regions 3 and 4, the following are also known to be highly tolerant in the regions in which they occur: *Cercopithecus p. petaurista, C. nictitans martini, Procolobus verus, Taurotragus eurycerus, Cephalophus niger, Dendrohyrax dorsalis sylvestris.* Of the remaining forms there is no assessment as yet, save that *Pan troglodytes verus* in the Gold Coast is apparently an exception: it is not tolerant of a wide range of ecological conditions.

In general, it can be stated that the poor fauna of "Western Nigeria" and "Togoland" comprises a majority of species-groups possessing a high degree of ecological tolerance. To such a great extent are the species-groups inhabiting the two regions identical, that it is logical to treat the whole of the High Forest between the Volta and the Niger as a zoogeographic unit.

The following are proposed as zoogeo-

graphic terms which may, it is hoped, have an application to problems other than the immediate one: within the Equatorial High Forest zone, or Western Sub-region of Sclater & Sclater (1899), a group of organisms is said to have a *central* distribution if it is found *only to the east of the Niger;* to have an *occidental* distribution if it is found *only to the west of the Volta;* to have an *interfluvial* distribution if it is found *between the Volta and the Niger;* to have an *ambisilvan* distribution if it is found *both east of the Niger and west of the Volta.*

Thus in terms of the categories used above, we can be more precise concerning the distribution of the various groups: *overall* groups are ambisilvan *and* interfluvial: *general* groups are usually simply ambisilvan, sometimes ambisilvan (discontinuous) and interfluvial; *endemic central* groups are simply central, or central *and* interfluvial; *endemic western* groups are occidental, or occidental *and* interfluvial. Examples of each type are illustrated in the maps in fig. 4.

Subdivision of these categories is possible, indeed obligatory in more detailed regional studies, but the use of these categories should simplify zoogeographic studies of the African High Forest in general.

The Interfluvial Fauna

The meager High Forest fauna existing between the Volta and the Niger will now be analyzed in terms of the lowest taxonomic categories, species and subspecies. Once again, only the Primates, Sciuromorpha, Artiodactyla and Hyracoidea are considered. Since it is necessary in this case to go into systematic detail rather more closely, the list of

Fig. 3. Percentage composition of the various elements of the fauna in the 6 regions. Shading as in figure 2.

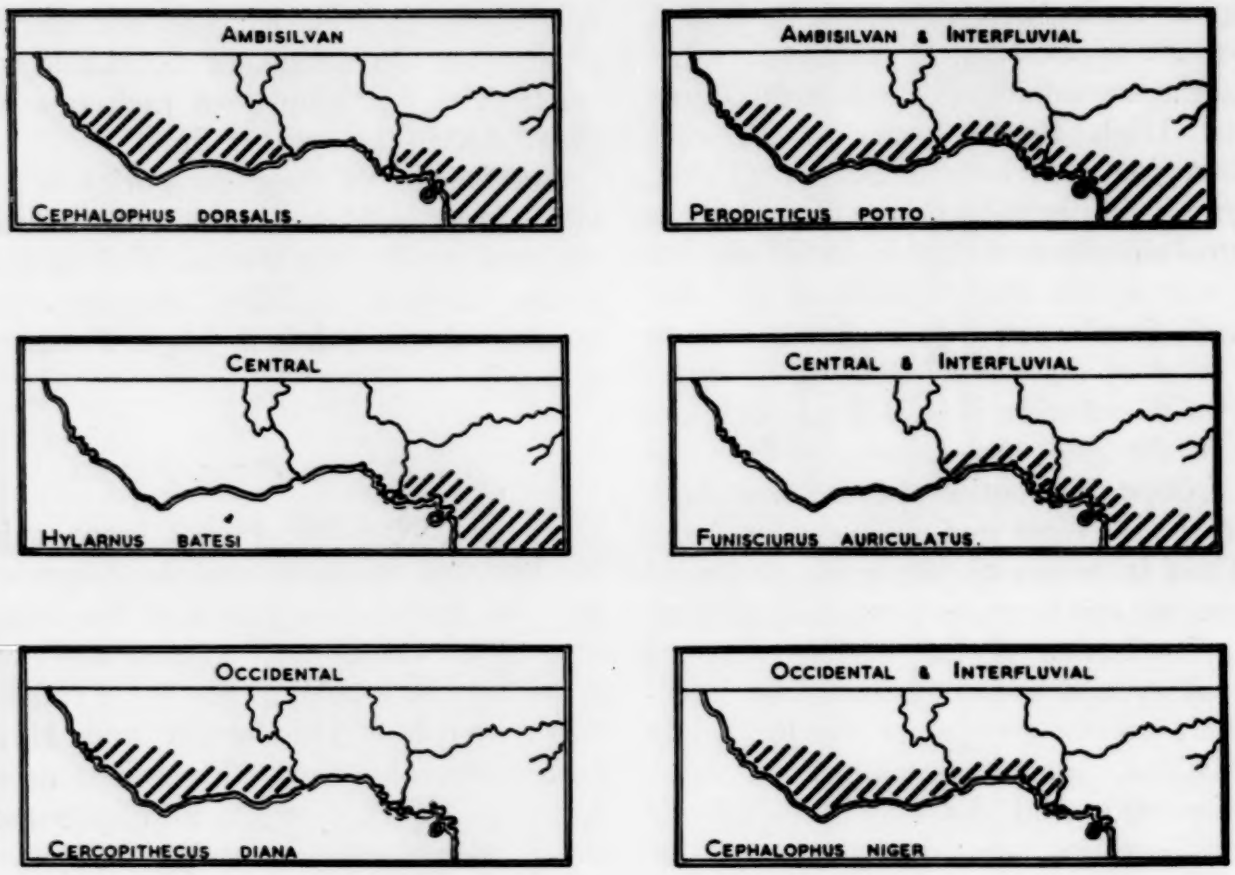

FIG. 4. Examples of various types of distribution.

fauna is given in full, with authorities. Detailed distribution data are to be found in Baudenon (1952), Booth (1956b, c), and Rosevear (1953).

Primates

Perodicticus potto potto (P. L. S. Müller), 1766.
Galagoides demidovii demidovii (G. Fischer), 1798.
Cercopithecus mona (Schreber), 1775.
C. petaurista petaurista (Schreber), 1774.
C. erythrogaster Gray, 1866. (*C. petaurista*-group).
C. erythrotis sclateri Pocock, 1904. (*C. cephus*-group).
C. nictitans martini Waterhouse, 1838.
Colobus polykomos vellerosus (I. Geoffroy), 1834.
Procolobus verus (van Beneden), 1838.
Pan troglodytes verus Schwarz, 1934.

Sciuromorpha

Anomalurus derbianus nigrensis Thomas, 1904.
Anomalurops beecrofti laniger (Temminck), 1853.
A. beecrofti argenteus (Schwann), 1904.
Funisciurus auriculatus oliviae Dollman, 1911.
F. anerythrus (Thomas), 1890, subsp. (*F. pyrrhopus*-group)

F. substriatus de Winton, 1899. (*F. pyrrhopus*-group)
F. raptorum Thomas, 1903. (*F. pyrrhopus*-group)
Heliosciurus rufobrachium isabellinus (Gray), 1867. (*H. gambianus*-group)
Protoxerus stangeri nigeriae (Thomas), 1906.

Artiodactyla

Potamochoerus porcus porcus (Linné), 1758.
Tragelaphus scriptus scriptus (Pallas), 1766.
Taurotragus eurycerus eurycerus (Ogilby), 1837.
Syncerus nanus (Boddaert), 1785.
Cephalophus ogilbyi brookei Thomas, 1903.
Cephalophus niger Gray, 1846.
Cephalophus silvicultor silvicultor (Afzelius), 1815.
Cephalophus maxwelli maxwelli (H. Smith), 1827. (*C. monticola*-group)

Hyracoidea

Dendrohyrax dorsalis sylvestris (Temminck), 1853.

Table 2 gives the affinities of these forms and their distribution in "Togoland" and in "Western Nigeria." Of the total of 28 forms, 13 are found in both territories, 6 in "Togoland" only and 9 in "Western Nigeria" only. If, however, as seems likely, *Funisciurus substriatus* proves to be a subspecies of *F. anerythrus*, and identical not only with the form of that species reported from "Western

TABLE 2. *Differentiation of the interfluvial fauna*

Species	Status	Togo race	Status	W. Nigeria race	Status
Perodicticus potto	A+I	*P. p. potto*	O+I	*P. p. potto*	O+I
Galagoides demidovii	A+I	*G. d. demidovii*	O+I	*G. d. demidovii*	O+I
Cercopithecus mona	C+I	*C. mona*	C+I	*C. mona*	C+I
Cercopithecus petaurista	O+I	*C. p. petaurista*	O+I	—	
Cercopithecus erythrogaster	I	—		*C. erythrogaster*	I
Cercopithecus erythrotis	C+I	—		*C. e. sclateri*	C+I
Cercopithecus nictitans	A+I	—		*C. n. martini*	C+I
Colobus polykomos	O+I	*C. p. vellerosus*	O+I	*C. p. vellerosus*	O+I
Procolobus verus	O+I	*P. verus*	O+I	—	
Pan troglodytes	A+I	—		*P. t. verus*	O+I
Anomalurus derbianus	A+I	—		*A. d. nigrensis*	C+I
Anomalurops beecrofti	A+I	*A. b. fulgens*	O+I	*A. b. argenteus*	C+I
Funisciurus auriculatus	C+I	*F. a. oliviae*	C+I	*F. a. oliviae*	C+I
Funisciurus raptorum	I(?)	—		*F. raptorum*	I
Heliosciurus rufobrachium	A+I	*H. r. isabellinus*	(C)+I	*H. r. isabellinus*	(C)+I
Protoxerus stangeri	A+I	*P. s. nigeriae*	I	*P. s. nigeriae*	I
Potamochoerus porcus	A+I	*P. p. porcus*	O+I	*P. p. porcus*	O+I
Tragelaphus scriptus	A+I	*T. s. scriptus*	O+I	*T. s. scriptus*	O+I
Taurotragus eurycerus	A+I	*T. e. eurycerus*	A+I	—	
Syncerus nanus	A+I	*S. nanus*	A+I	*S. nanus*	A+I
Cephalophus ogilbyi	A+I	*C. o. brookei*	O+I	—	
Cephalophus niger	O+I	*C. niger*	O+I	*C. niger*	O+I
Cephalophus silvicultor	A+I	*C. s. silvicultor*	A+I	*C. s. silvicultor*	A+I
Cephalophus maxwelli	O+I	*C. m. maxwelli*	O+I	*C. m. maxwelli*	O+I
Dendrohyrax dorsalis	A+I	—		*D. d. sylvestris*	O+I

A = ambisilvan.
C = central.
O = occidental.
I = interfluvial.

These terms are defined on p. 55.

Nigeria," but also with *F. mandingo nigrensis* from Eastern Nigeria, the above figures will become modified. It suffices to point out that the systematics of the *F. pyrrhopus*-group is at the moment chaotic. Hence no attempt has been made in Table 2 to assign eastern or western affinities to the above two forms.

Togoland has no endemic species or races. "Western Nigeria," on the other hand, appears to have two, namely *Cercopithecus erythrogaster* and *Funisciurus raptorum,* which are found only in that region. It is therefore likely that the purely interfluvial *Protoxerus stangeri nigeriae* also originated in "Western Nigeria," and it is possible that the same applies to *Cercopithecus erythrotis sclateri* and *Heliosciurus rufobrachium isabellinus.*

There is only one case in which "Western Nigeria" and "Togoland" apparently contain separate subspecies of the same species: the occidental *Anomalurops beecrofti laniger* occurs in "Togoland," while the central *A. b. argenteus* is found in "Western Nigeria."

Discounting the problematic *Funisciurus* spp., the affinities of the elements of the interfluvial High Forest fauna may be summarized as follows:

Togoland: 18 forms. —3 ambisilvan; 11 identical with occidental "Gold Coast" forms; 2 probably endemic interfluvial ("Western Nigeria") forms (*Heliosciurus rufobranchium isabellinus* and *Protoxerus stangeri nigeriae*); 2 probably of central origin (*Cercopithecus mona, Funisciurus auriculatus oliviae*).

Western Nigeria: 21 forms. —2 ambisilvan; 9 identical with occidental "Gold Coast" forms; 5 probable endemics; 5 probably of central origin.

The remarkable feature of the distribution of interfluvial High Forest mammals is the number of occidental forms which occur in "Western Nigeria." Most of these are replaced by other species or races in "Eastern Nigeria," although, as we have seen, *Cephalophus niger* is quite distinct endemic occidental group. This, of course, suggests the importance of the Niger as a geographic barrier during the evolution of the West African fauna.

Discussion

The equatorial High Forest of Africa is, both from the animal and plant viewpoint, a substantially homogeneous environment. Nevertheless, a considerable degree of differentiation of both flora and fauna has taken place, as between the various geographic regions within the zone. At present, few geographic barriers exist within the zone, and even large rivers such as the Congo and the Niger are generally only partially effective barriers. The Dahomey Gap, as a break in the continuum, has been frequently cited (e.g., by Aubréville, 1949a; Dekeyser, 1955 and others). The present existence of the Dahomey Gap is due, at least in part, to the dry climate of the coastal belt in that region. It is clear, however, that the climate has not always been so dry, or there could have been no ambisilvan elements of the flora and fauna. It must be accepted that climatic fluctuation has taken place. Generally speaking, geologists, archaeologists, botanists and zoologists are all agreed in admitting the existence of such fluctuations, more especially during the Quaternary. Brückner (1955), working in the Gold Coast, finds evidence from the differentiation of the superficial mantle rock which leads him to postulate the occurrence of three periods of humid climate, corresponding to the pluvial periods of Leakey (1936). Intercalated with these humid periods are two interpluvials, during which the climate was very much drier. The pluvials have been held to be contemporaneous with the glacial periods in the northern hemisphere, and the interpluvials with the interglacials, but a strict correlation remains to be established.

Aubréville (1949b), adduces a further hypothesis. In his view, climatic change, which he admits to have taken place, has been the result of the shifting of the equator from a position well to the north

of that which it occupies at present. Its present position was not achieved by a single southward migration, but only after some oscillation, including at least one distinct southward swing. Each oscillation of the equator, according to this theory, would carry the equatorial High Forest belt with it, thus tending to increase or reduce the depth of the belt on the Guinea Coast. At the southernmost point of its migration, the High Forest of the Guinea Coast was reduced to three refuges, one in Liberia, one just west of Cape Three Points, and one in the Niger delta and Calabar, which was continuous with the main central forest block.

Aubréville's theory in some respects goes further than is really necessary for the present purpose, and in effect only supplements the geological evidence. The southward migration of the equator is held to have occupied practically the whole of the Tertiary period, but it is not clear how recent were the oscillations.

To return to the zoogeographic data: it is clear that the scattered distribution of some of the species groups may be explained as a result of the retreat of the High Forest to refuges of the type postulated by Aubréville, under the influence of dry climatic conditions. Following the amelioration of climate, the forest, and with it the forest fauna, would advance once more. The extent of the recovery of former range would depend upon various factors, including initial population size and density, ecological status, and geographic barriers.

Extreme isolation is shown in the case of the *Cercopithecus diana-* and *C. petaurista*-groups. In the former case, the two species concerned are *diana,* an occidental species, and *dryas,* restricted to a small area in the Upper Congo. In the latter, *C. petaurista* and *C. erythrogaster* are found only west of the Niger, while *C. ascanius* has a wide range in the Upper Congo basin, but is absent from Middle Congo and "Gaboon." To isolation of such a degree, one or more very severe dry periods probably contributed.

That "Gaboon" also contained an important refuge is also fairly certain. *Papio sphinx* and *Zenkerella insignis* are restricted to that region, as also are a few groups belonging to other Orders. At the same time, "Gaboon" shares with "Gold Coast" and "Liberia" the *Epixerus ebii*-group. The *Gorilla gorilla*-group has spread beyond the confines of the Gaboon region as defined above, but in the Belgian Congo it is absent over most of the High Forest, only reappearing in the Upper Congo (Lake Kivu region especially).

During the period when contemporary species and species-groups were differentiating, it would appear that there is evidence for the existence of three important refuges, probably situated in, but certainly supplying the modern fauna of, "Liberia," "Gaboon" and the Upper Congo. Within the area with which we are more particularly concerned, there would be no need to postulate the existence of any High Forest at all in "Western Nigeria" or "Eastern Nigeria" during severe dry periods, were it not for the isolation in the Cameroons Mountains area of *Cercopithecus l'hoesti,* possibly *Procolobus badius,* and the unique *Heliosciurus cooperi.* All the remainder of the "Eastern Nigeria" fauna could have been supplied from "Gaboon," and has for the most part undergone only subspecific differentiation from that of "Gaboon" itself. In many cases, there has been no taxonomically recognizable differentiation at all, only a relative poverty of the fauna.

"Liberia" has clearly formed the main refuge of the occidental fauna during severe dry periods, since it possesses *Cercopithecus nictitans stampflii,* and the very distinct *Cephalophus zebra* and *C. jentinki,* all of which are absent from "Gold Coast."

Lacking any accurate measure of evolutionary rates in mammals, it is impossible to date the beginning of isolation and differentiation of the various groups. We have the example of *Phoca vitulina* investigated by Doutt (1942), which ap-

pears to have become differentiated at the subspecific level in complete isolation in between 3,000 and 8,000 years. Simpson (1944) also quotes a period of one to two million years as having sufficed for the differentiation of fully distinct genera of Procyonids, Cricetines and Cervids in South America. The occidental fauna possesses possibly two distinct genera. One, *Micropotamogale,* is so recently discovered that a balanced assessment of its generic status is not as yet available. The other, *Xiphonycteris,* is as yet known only from the type, and, like many Microchiroptera, its distribution may yet be found to be wider. Allowing for the fact that rates of evolution will differ with the group concerned, there is no necessity to assume that the partially independent evolution of an occidental mammalian fauna commenced any earlier than the latest Pliocene, and it may well have taken place entirely within the Quaternary.

As Aubréville (1949a) has pointed out, the present Dahomey Gap lies at that point on the West African coast where the coastline is most nearly parallel to the prevailing southwest wind. This wind, which represents a landward diversion of the southeast trades, can, *provided the position of the equator was not far to the north of its present position,* be assumed to have been the principal rain-bearing wind throughout the Quaternary. As Aubréville's hypothesis concerning the movements of the equator is not inconsistent with this assumption, we may also infer that it is likely that throughout the Quaternary increasing desiccation has most severely affected the region of the present Dahomey Gap. This area must have been deprived more than once of its High Forest and the accompanying fauna. The Gap, always centered on Dahomey, was probably at its widest during the two interpluvials, stretching from the Kroo Coast to the Cameroons. During the pluvials, it may well have been completely closed, and the High Forest probably extended much farther inland than it does today. This region has probably been affected, however, not only by the extreme desiccation of the interpluvials, but also by minor fluctuations in climate, less drastic and of shorter duration. Zeuner (1945) in particular has shown that the Pleistocene climate was highly dynamic, fluctuating over quite short periods within the major phases. There is no reason to suppose that this was not the case in West Africa also. Leakey (1936) would appear to have adduced evidence for such fluctuations in East Africa.

The present interfluvial fauna is poor, at least partly as a result of being bounded by the two greatest rivers in West Africa. The recovery of the fauna from the last presumed dry period has been incomplete; to the east, the Niger must to a certain extent have prevented the recolonization of "Western Nigeria," to the west the Volta must have had the same effect upon the fauna of "Togoland." "Western Nigeria" has more occidental forms than any other single category. The Niger is therefore likely to have been a more important barrier than the Volta. On the other hand, all the true Squirrels of "Togoland" originate from "Western Nigeria" or from farther east, and the occidental races of the Tree Hyrax and the Chimpanzee are present in "Western Nigeria," though absent from "Togoland." Both are replaced by central races in "Eastern Nigeria."

In view of this situation, we must postulate that the most recent dry period was relatively mild, and involved an incomplete destruction of the interfluvial High Forest and its fauna. A refuge must have been formed, most likely in "Western Nigeria," permitting the survival of the Tree Hyrax and Western Chimpanzee, and the probable differentiation as separate forms of the Monkeys and Squirrels described as endemics. This refuge may have been in the Benin area, described by Aubréville (1949a) as having very nearly a true rain-forest

climate today, or it may have been in edaphic riparian forest on the right bank of the Niger itself.

Apart from those forms which give clear evidence of their having differentiated or survived in such a refuge, it is likely that there were other survivals which, by reason of their non-differentiation and present continuous distribution, have left no trace of their migrations. *Perodicticus potto, Galagoides demidovii, Potamochoerus porcus, Tragelaphus scriptus, Syncerus nanus, Cephalophus silvicultor, C. niger* and *C. maxwelli* probably all come into this category. The case of *Cercopithecus mona* is doubtful.

The fauna of "Togoland" is derived mainly from the occidental "Gold Coast" forms, but also in part from that of "Western Nigeria." The presence of "Western Nigeria" Squirrels is explicable as a result of the failure of the "Gold Coast" forms to cross the Volta (except for the gliding *Anomalurops*). The Squirrels from the "Western Nigeria" refuge had no comparable barrier to cross, and following forest connections were able to colonize the whole area between the Niger and the Volta. On the other hand, the Monkeys, except for *Cercopithecus mona,* are of "Gold Coast" origin. Monkeys are excellent swimmers, though the Galagos and the Potto are probably poor performers and so, by reputation, are the Chimpanzee and other Apes. The Artiodactyla are also good swimmers, but the Tree Hyrax is probably not. Though some of the Artiodactyla of "Togoland" could have come from "Western Nigeria," there are two which could not, namely *Cephalophus ogilbyi* and *Taurotragus eurycerus.*

The distribution data would appear to suggest that it is the Niger and the Volta which form the most important zoogeographic barriers in present-day West Africa, the Niger being distinctly the more important. The Dahomey Gap in its present form is apparently of less importance, but in the past must have had a considerable influence on the differentiation of the occidental from the central fauna. Situated in the region most sensitive to climatic change throughout the Quaternary, its vegetation cover and its mammalian fauna are liable to have been subjected to repeated fluctuations. Its main contribution to the differentiation of the High Forest fauna has been in acting as an isolating region at times when the climate was considerably drier than it is today and the High Forest vegetation completely destroyed throughout the area.

Summary

1. The distribution of species-groups of Primates, Sciuromorpha, Artiodactyla and Hyracoidea in West African High Forest is given in detail.

2. Four types of distribution are recognized:

a) *ambisilvan,* groups which occur both east of the Niger and west of the Volta.

b) *central,* groups which occur only east of the Niger.

c) *occidental,* groups which occur only west of the Volta.

d) *interfluvial,* groups which occur between the Niger and the Volta, and which may have their origin from groups of type a), b) or c).

3. The central fauna is much richer than the occidental, which, though it contains a small number of endemic groups, is nevertheless thought to have been derived originally from the former.

4. The interfluvial fauna is remarkably poor. The zoogeographic data tend to corroborate geological evidence for the periodic deterioration of the climate between the Niger and the Volta during the Quaternary, which probably deprived the area of its High Forest several times, either partially or completely.

5. Climatic fluctuation has resulted in the Dahomey Gap acting as an important isolating mechanism in the past. Today, it is probably less important than the Volta and Niger rivers.

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EVOLUTION AND VARIATION IN *TRILLIUM*. II. VARIATION IN SOME EXTERNAL CHARACTERS OBSERVED IN NATURAL POPULATIONS OF *TRILLIUM KAMTSCHATICUM PALL.*

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Studies on chromosomal variation in natural populations of *Trillium kamtschaticum Pall* have been carried out by several authors (Haga & Kurabayashi, 1953; Kurabayashi, 1957). They found structural changes in chromosomes of this plant by means of the differential staining reaction in chromosomes. The patterns in chromosome segments detected by means of this reaction varied not only from population to population but also within individual populations. These authors, after comparison of inter- and intrapopulational variation in chromosome patterns, found that 1) the variability in each population increased with its size, and 2) there were local differences in the distribution of individual chromosome patterns. The former finding was examined in detail, based on general principles of population genetics, by Hiraizumi (1956) and Narise (1956). They concluded that the variation in natural populations of this plant was determined, as suggested by the previous authors (Haga & Kurabayashi, 1954), principally by the influence of random genetic drift.

Analysis of variations in some external characters of this plant in these populations was carried out, side by side with the chromosome studies, by the present author with the cooperation of several other investigators from the same laboratory. The results will be described below and compared with those obtained by chromosomal analysis.

MATERIALS AND METHODS

More than fifty sample plants were taken at random from each of the natural populations of various localities in northern Honshu and Hokkaido (fig. 1). Examinations of the characters were usually made with plants taken directly from their native habitats. But sometimes, plants kept for one to three years after transplantation from the native habitats to the station at Sapporo were used. Preliminary tests showed that there was no detectable difference in the characters chosen for this study, between the plants taken directly from their native habitat and those examined after transplantation.

The characters chosen for investigation were the longitudinal diameter of stomata, the ratio of length to width of petals, sepals, and leaves, and that of length to diameter of the fruits (fig. 2).

The measurement of stomata was made by making 600× Camera-Lucida drawing of stomata from the abaxial epidermis of the leaf blade. Data on fruits were obtained by measuring ripe fruits with calipers. The other measurements were made from blue prints taken at the stage of full bloom.

RESULTS AND DISCUSSION

The results obtained by this examination of external characters revealed a parallelism with those obtained by the examination of chromosomal composition of the populations in two respects. First, the variance of the external characters of the populations changed in accordance with the degree of variability of chromosomal composition (represented by N. T.C. in table 1).

Second, the mean values of the characters obtained within a population belonging to one of the three population

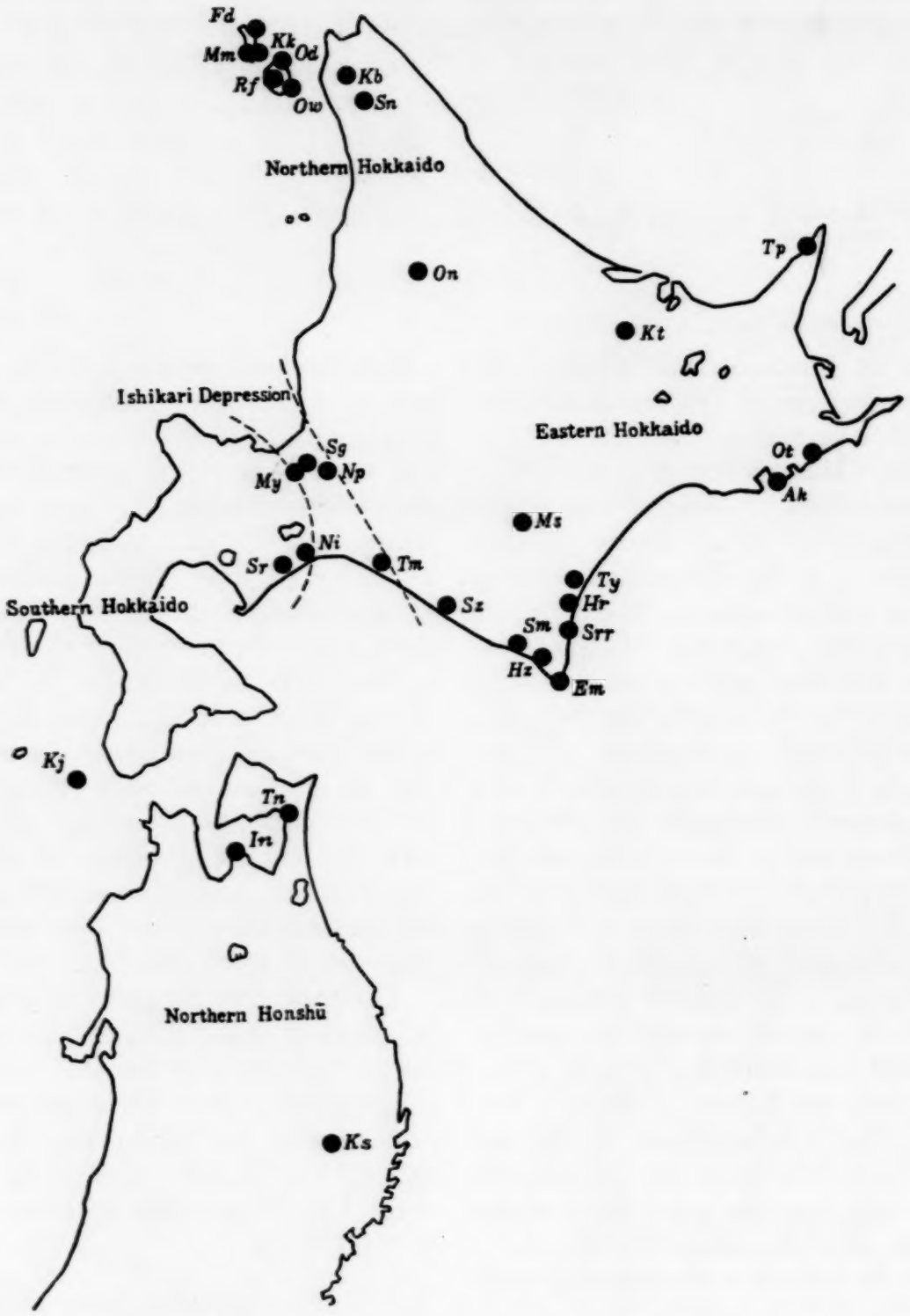

FIG. 1. Map of Northern Japan representing the localities from which natural populations of *T. kamtschaticum* were chosen for the investigation.

groups, which were established on the basis of differences in chromosomal composition (Kurabayashi, 1957), nearly coincided with each other and differed more of less from those obtained in populations belonging to the other groups.

Such a situation seems to indicate the existence of some underlying mechanism responsible for the manifestation of the parallelism. It is impossible at present to determine the mechanism by direct analysis, since the results obtained were not experimental but were from observation of natural populations in native habitats. Accordingly an attempt was made to ascertain the mechanism indirectly.

The principal mechanism leading to

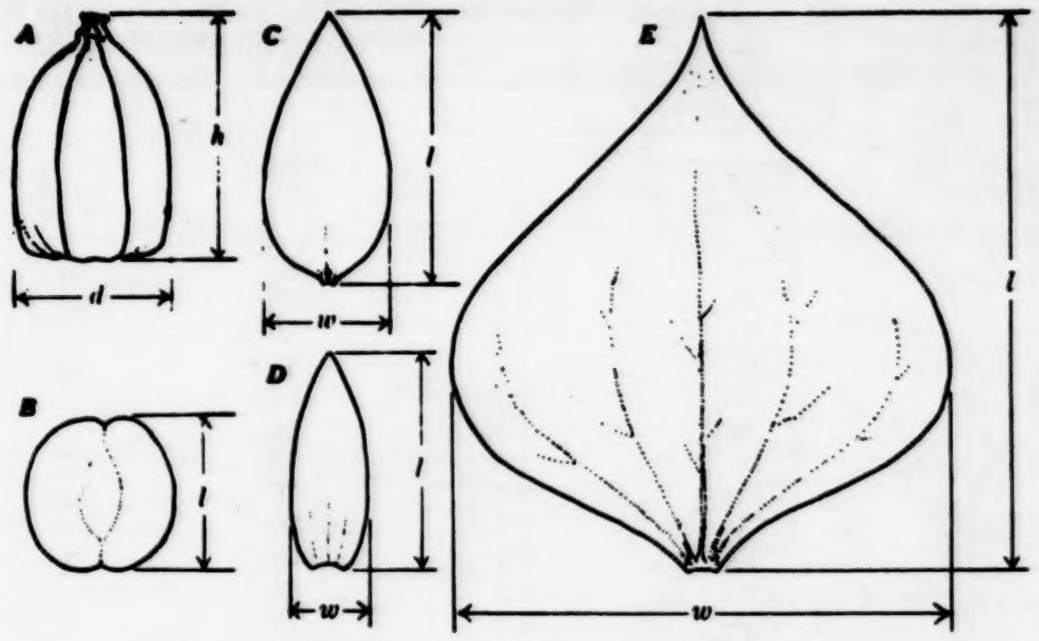

FIG. 2 A–E. Schematic representation of the characters chosen for investigation. A: Fruit, B: Stomata, C: Petal, D: Sepal and E: Leaf. (Reduced or enlarged arbitrarily.) d: diameter, h: height, l: length, w: width.

differences in homogeneity in chromosomal composition among natural populations of this plant is, as pointed out by Hiraizumi and Narise, random genetic drift. If the variations in the above described characters include heritable ones, they must indicate qualitatively, the same populational changes as the chromosomal composition. However, there may be some quantitative differences between the two variables, chromosomal homogeneity and variance in external characters, when both are under the influence of random genetic drift of identical intensity. This is because the former depends on the fixation of the equivalent of

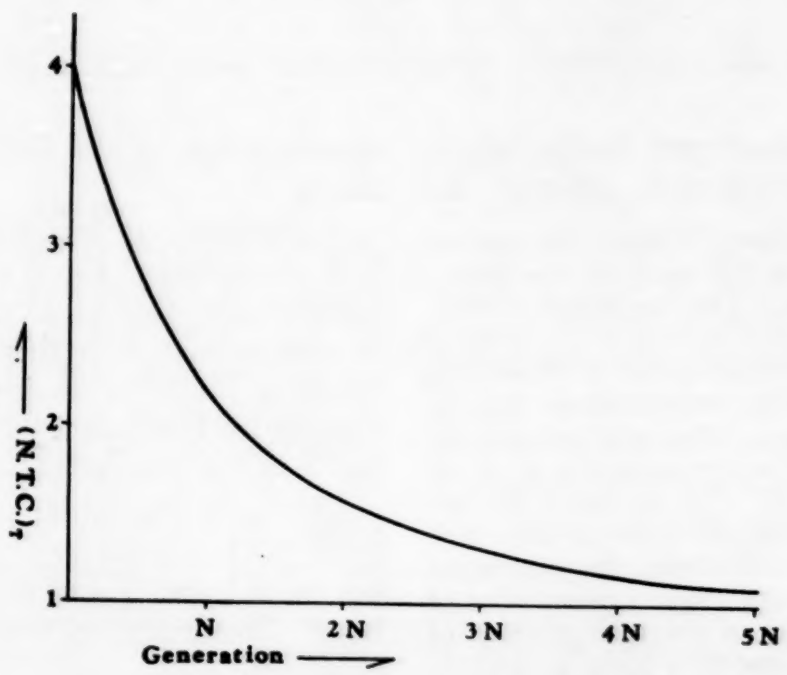

FIG. 3. The calculated decrease in N.T.C. with time time measured in generations. The unit of measurement is N. the population number (Hiraizumi, 1956).

TABLE 1. *The percentage of fixed loci calculated from the N.T.C. value variance of the external characters in natural*

Population name	Abbreviated name of population	N.T.C.	Fixed loci in %	Leaf	
				No. of plants analysed	Variance (10^{-6})
Kusakai	*Ks*	1.0	100	50	861
Nishikioka	*Ni*	1.0	100	50	677
Kojima	*Kj*	1.0	100		
Rishirifuji	*Rf*	1.2	85	48	872
Funadomari	*Fd*	1.2	85		
Onnebetsu	*On*	1.2	85		
Ino	*In*	1.4	70	27	1,817
Tomikawa	*Tm*	1.4	70	41	1,572
Oniwaki	*Ow*	1.5	70		
Kafuka	*Kk*	1.6	65		
Shiraoi	*Sr*	1.6	65		
Oshidomari	*Od*	1.9	45		
Shimonuma	*Sn*	2.0	45		
Momoiwa	*Mm*	2.2	35	50	810
Minamisatsunai	*Ms*	2.3	35		
Kabutonuma	*Kb*	2.3	35		
Maruyama	*My*	2.4	35		
Tanabu	*Tn*	2.5	30	32	1,258
Hiroo	*Hr*	2.9	25	55	2,007
Toyoni	*Ty*	3.0	20	50	2,583
Nopporo	*Np*	3.0	25	25	2,151
Horoizumi	*Hz*	3.0	20	50	3,093
Sapporo Genshirin	*Sg*	3.1	20		
Kitami	*Kt*	3.2	15		
Saruru	*Srr*	3.2	15	36	3,261
Erimo	*Em*	3.2	15	50	3,088
Teppanbetsu	*Tp*	3.6	10	45	889
Ochiishi	*Oi*	3.9	5	50	2,416
Akkeshi	*Ak*	3.9	5		
Shizunai	*Sz*	4.2	0	30	3,241
Samani	*Sm*	4.2	0		

four multiple alleles[1] and in the latter, with genes that presumably influence the manifestation of the characters quantitatively.

Accordingly it becomes necessary, before comparing the two variables, to calculate the rate of fixation of gene loci in comparison with that of chromosome patterns, the latter having been computed already by Hiraizumi (1956 and see also fig. 3 in the present paper).

Let L_0 be the initial proportion of unfixed loci (assuming two allelomorphs per locus) and T the number of generations. According to Wright (1931), the

[1] The different patterns of each chromosome pair are equivalent, in the mode of inheritance, with multiple alleles. The maximum number of different chromosome patterns or types found among the natural populations of *T. kamtschaticum* were found to be, on an average, four in each chromosome pair. This was assumed by Hiraizumi (1956) to be the number with which the population started. He computed the assumption that the four different patterns may be regarded as multiple alleles, the number of generations necessary to attain a given value of N.T.C. N.T.C. is ⅕ of the total number of chromosome types found in a given population. Five being the number of homologous pairs of *T. kamtschaticum*. The value was used by him and in the present paper as an indication of homogeneity of an individual population of *T. kamtschaticum* (cf. Hiraizumi, 1956). The mode of random genetic drift in multi-allelic locus was also studied and discussed in detail by Kimura (1955, 1956).

(*a measure of chromosome heterogeneity, Hiraizumi, 1956*) *and the populations of* Trillium kamtschaticum

Sepal		Petal		Fruit		Stomata	
No. of plants analysed	Variance (10^{-6})	No. of plants analysed	Variance (10^{-6})	No. of plants analysed	Variance (10^{-6})	No. of plants analysed	Variance (10^{-6})
51	871	51	1,220	16	915	50	96
50	1,287	50	978	31	413	30	176
10	1,791	10	534				
51	1,153	51	1,405	35	344	50	133
25	2,675	26	845	19	281	40	420
				15	571	20	377
12	1,187	12	847	7	304	30	291
50	1,777	50	1,725	17	665	50	377
				30	471		
				42	522	50	459
						35	523
50	2,943	50	1,641	20	683	40	146
						25	672
		50	1,283	10	1,487		
50	4,703	50	2,124	18	1,739	30	843
23	2,442	24	1,516	20	1,198	40	636
		22	2,684	28	1,259	20	648
48	2,528	48	1,823	8	1,025	20	616
		50	2,132				
50	4,292	50	2,356	50	1,834	50	861
		27	2,464				
50	2,351	50	2,629	23	1,661	49	845
25	2,680	25	2,765	38	1,922	30	807
				37	1,277		
50	3,029	50	2,495	43	1,898	27	1,130
55	3,730	55	2,903	57	2,276		
				35	3,192		
21	2,175	21	2,351	35	2,015	50	983
						40	1,089
		44	3,104			50	979
				51	3,196	30	1,208

percentage of unfixed loci in the T'th generation is given by $L_t = L_0 e^{-t/2n}$, where N is the effective population number. The values of T in each population investigated in the present paper can be calculated, on the basis of their N.T.C. values, with N, from the curve in figure 3. It becomes possible, then, utilizing these T values, to obtain the percentages of fixation of pairs of allelomorphs (table 1). Utilizing the percentage values, an attempt was made in the following to compare the variance with the corresponding value of the percentage of fixation of pairs of allelomorphs (fig. 4).

Approximately a linear relation was found between the two variables. The variance may be expected to increase linearly with the proportion of unfixed loci, if there is no dominance or epistasis among the pairs of allelomorphs or polygenes, and if they recombine freely.

Such seem rather inconceivable conditions, of which no examination is possible at present. Further the variance obtained must not be wholly genetic but must be partly environmental. In the present materials, however, the latter seems not to disturb seriously the results represented in figure 4 because the environmental modification of the characters chosen for investigation was not large,

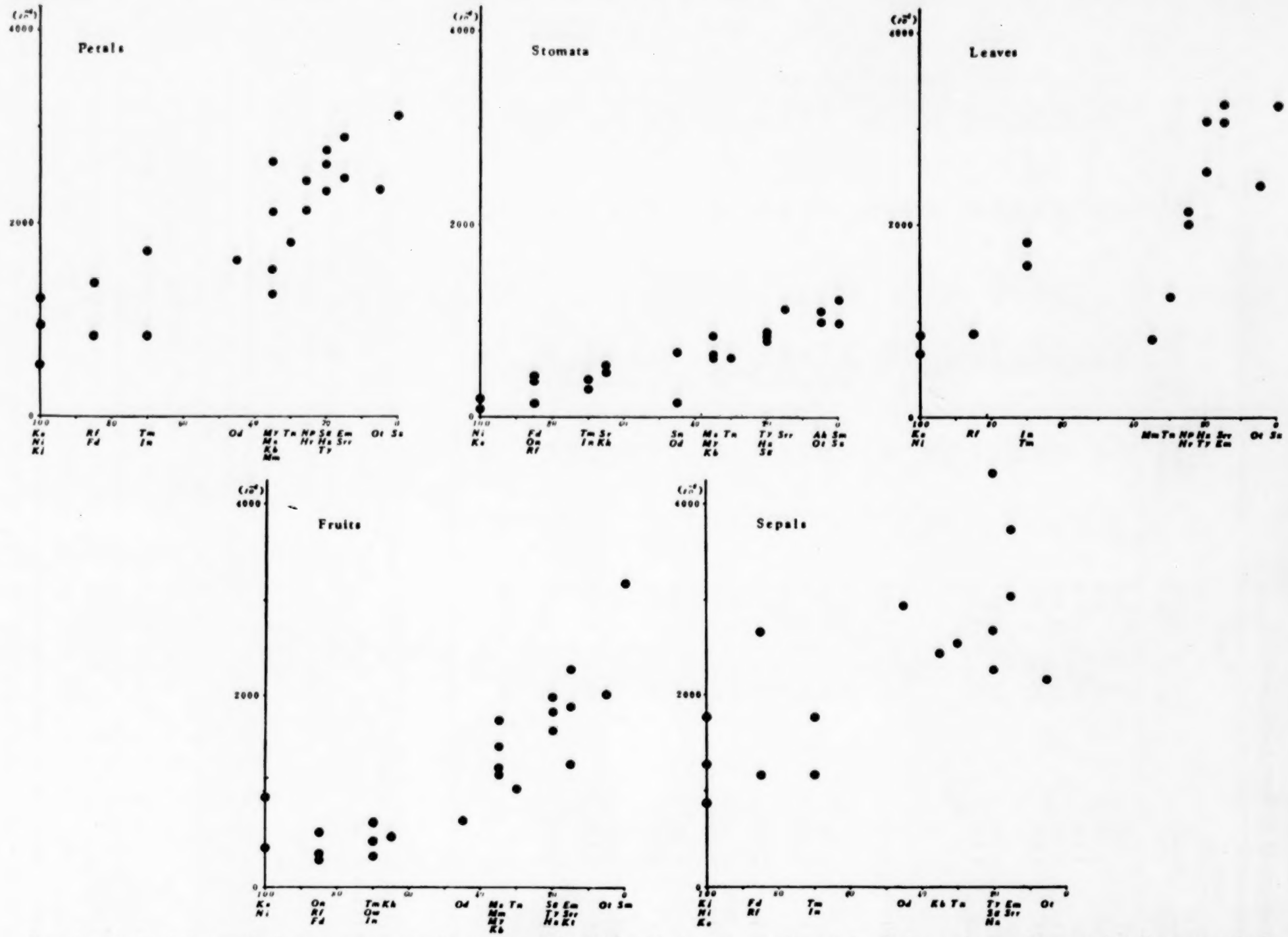

FIG. 4. Each of the vertical axes represents the variance obtained with leaves, sepals, petals, fruits and stomata guard cells, respectively. The variance was obtained after transformation of each ratio to logarithms, which made the variance less correlated with the mean. The horizontal axes represent the computed percentage of fixed gene loci. The variance in each population is shown by black circles in the position of the corresponding percentage values of the fixed loci. Note the approximately linear increase in the variance in proportion to the decrease in the percentage of fixation.

TABLE 2. *Chromosal composition (represented by percentage of types of chromosome D detected in each of the populations) and the mean values of the external characters among populations in different population groups of* Trillium kamtschaticum

Population group	Type No.	Frequencies of detected types of chromosome D									Mean values of external characters				
		1	15	3	4	5	6	7	2	8	Leaf	Sepal	Petal	Fruit	Stomata
	Ks			100							1.19	3.13	1.87	1.18	58.0 (mm)
	In			100							1.25	2.95	2.02	1.29	64.6
South	*Tn*			100							1.20	2.99	2.03	1.33	62.9
	Ki							100				2.74	2.16		
	Sr							100							62.1
	Sz	20			6	47		9	12		1.07		1.87		55.5
	Sm	7				26	39	14	8					1.59	58.7
	Em	13				81					1.10	2.68	1.64	1.73	
	Hz					55					1.03	2.73	1.57	1.59	57.8
	Srr					100					1.36	2.98	1.66	1.51	59.5
East	*Ty*					100					1.18	2.99	1.76	1.55	58.3
	Hr					92					1.01		1.66		
	Ms				6	94						2.72	1.46	1.57	62.0
	Ak	20				76									56.1
	Ot					100					1.17	2.61	1.75	1.77	57.8
	Tp	37			21	26				11	1.02			1.63	
	Kt	100												1.70	
	On	100												1.46	64.6
	Sn	100													56.4
	Kb	100										2.87	1.87	1.39	56.9
	Od	100										2.47	1.86	1.36	58.4
North	*Ow*	100												1.21	
	Rf	100									1.07	2.46	1.73	1.37	57.8
	Kk	100												1.45	62.3
	Fd	100										2.92	2.00	1.49	60.2
	Mn	100									1.12		1.65	1.54	
	Np	45		55							1.00		1.92		
Ishikari	*Sg*	76	24									3.26	1.87	1.46	64.8
	My	42	47	11									1.76	1.47	63.4
Depression	*Tm*	100									1.15	2.83	1.86	1.35	53.7
	Ni			100							1.62	3.99	2.26	1.29	65.8

The variance was obtained after transformation of each ratio to logarithms, which made the variance less correlated with the mean. The horizontal axes represent the computed percentage of fixed gene loci. The variance in each population is shown by black circles in the position of the corresponding percentage values of the fixed loci. Note the approximately linear increase in the variance in proportion to the decrease in the percentage of fixation.

as shown in the preliminary examinations carried out in different environmental conditions.

The variance may be affected also by selection and mutation. These may, in cooperation, alter the linear relation between the two variables in different ways in the different characters investigated. The influence of these factors was also left unexamined. But it seems plausible that the characters chosen were more or less neutral selectively. Deviations from linearity were most marked in the case of leaves and sepals, next in petals and fruits and least in stomata guard cells (fig. 4). Even in the case of the maximum deviation, however, the general aspect of the relation between the two variables was approximately linear. That is to say, the variability of the external characters among individuals of a given population of *T. kamtschaticum* may be regarded as being affected, primarily, in the same way as the variability of the chromosomal composition, due to random genetic drift.

The parallelism in another respect, viz., in local differentiation of the mean values of the characters and the chromosomal composition (table 2) may be regarded as the result of some correlative effect of isolation.

The natural populations of *T. kamtschaticum* hitherto investigated were grouped,

according to their chromosomal compositions, into three local groups; *South, East* and *North,* respectively, occupying northern Honshu and southern Hokkaido, eastern Hokkaido, and northern Hokkaido (Kurabayashi, 1957, table; and fig. 1, table 2 in the present paper). The populations investigated in the present study are listed, in table 2, according to this grouping and the mean values of their external characters are compared. The shape of fruit was the longest in *East,* next in *North* and the shortest in *South.* The shape of petals was widest in *East,* next in *North* and the narrowest in *South.*

The mean values of the other characters, however, did not show such correlative changes with the geographical chromosomal differentiation, and the intra-group variation of the mean values often exceeds the inter-group. Such a situation is in accord with that revealed by the chromosomal composition of the three geographical population groups. That is, the differentiation among these population groups was marked with respect to some chromosomes but not so with others (cf. Kurabayashi, 1957, table 19). Characters determined by genes or gene groups located on chromosomes which reveal marked difference in the mode of local distribution may reveal a local differentiation corresponding with that of the chromosomes.

The local differentiation of chromosomes was described only with respect to the differential chromosome segments which revealed detectable structural changes, while the external characters chosen here are determined by genes whose number and loci are not known. Thus, it is impossible here to go further into the nature of the correspondence between the chromosomal and morphological diversifications. It may, however, be permissible to expect that, with more genetic information, it may become possible to show more completely the mechanism of the parallelism. The two methods of the analysis, chromosomal and morphological, are, in this sense, mutually complementary in approaching the final solution.

The populations distributed along the Ishikari Depression (fig. 1, table 2) are under the influence of complicated migration and genetic drift (Tajima & Fukuda, 1956). The mean values of each of the characters reflect that situation well, some characters being intermediate among the three groups and others exceeding the variation range of the latter.

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Summary

The variation in five external characters was examined with plants obtained from natural populations of *Trillium kamtschaticum Pall.,* and the results obtained were examined in comparison with the chromosome compositions of the corresponding natural populations. Definite parallelism was seen between the variance of the characters and the heterogeneity of chromosomal composition in each of the populations investigated. Some of the external characters revealed local variations which were analogous with those detected by chromosomal analysis.

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SEXUAL ISOLATION AND VARIATION IN MATING BEHAVIOR WITHIN *DROSOPHILA ATHABASCA*

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Drosophila athabasca Sturtevant and Dobzhansky 1936 is a member of the *affinis* subgroup (Subgroup b) of the *obscura* group of the subgenus Sophophora (Patterson and Stone, 1952). It is widely distributed in the forests of northern North America from Alaska to eastern Canada and southward in the mountains to New Mexico in the west and to Tennessee in the east (Sturtevant and Dobzhansky, 1936; Novitski, 1946). The original description of this species included the recognition of an eastern subspecies, *mahican,* with somewhat lighter pigmentation than the western form. However, Novitski (1946), who studied the salivary gland chromosomes of both western and eastern *athabasca,* found no evidence that the subspecific designation should be maintained for the laboratory stocks at his disposal; neither morphological differentiation nor detectable reproductive isolation distinguished these western and eastern stocks.

D. athabasca is rather difficult to maintain in the laboratory, though it sometimes breeds well enough. Yields of flies per culture container vary widely, presumably due to microenvironmental variation, and stocks are frequently lost. By 1954 none remained of the older laboratory strains of *athabasca,* such as those studied by Sturtevant and Dobzhansky (1936), Novitski (1946), and Miller (1950a, 1951). In recent years a number of new cultures have been established, and attempted crosses between these have shown that a fairly high degree of sexual isolation exists between certain geographically different strains. Moreover, an aspect of mating behavior, duration of copulation, has been found to vary widely in these strains. Although the available information is not sufficient to show the pattern of this variation, the data are presented here on the grounds that they do establish the existence of appreciable intraspecific sexual isolation and mating behavior variation in this widely distributed North American species.

SEXUAL ISOLATION IN "NO-CHOICE" COMBINATIONS INVOLVING WYOMING AND MICHIGAN STRAINS

In the summer of 1954 new strains were established from collections at the Jackson Hole Biological Research Station near Moran, Wyoming, and at the University of Michigan Biological Station (U.M.B.S.) near Cheboygan, Michigan. To study the inheritance of a mutant character (rough eyes) that appeared in one of the Michigan strains, a few crosses were attempted between mutant Michigan females and normal Wyoming males. None of these produced any progeny. Additional attempts to make the two reciprocal crosses between Wyoming and Michigan *athabasca* also failed, though several strains of each kind were used. (Unfortunately, the mutant strain died out before it could be used in more extensive crosses, so the interlocality crosses had to be performed largely with wild type strains.)

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TABLE 1. *Cases of* D. athabasca *females inseminated after 10 or 11 day cohabitations in "no choice" (one kind of female, one kind of male) combinations involving Wyoming and Michigan (U.M.B.S.) strains*

(The number in parentheses after each combination indicates the number of strain combinations included in the pooled data.)

Combination	Number of females	Females inseminated	
		Number	Per cent
Wyoming ♀ × Wyoming ♂ (5)	182	136	75
Michigan ♀ × Michigan ♂ (6)	193	133	69
Wyoming ♀ × Michigan ♂ (12)	242	2*	1
Michigan ♀ × Wyoming ♂ (14)	233	0	0

* Adult hybrids accompanied one of these cases.

The existence and degree of sexual isolation were next investigated by way of 10 and 11 day combinations of one kind of female with one kind of male (both intra- and inter-locality) followed by examination of the seminal receptacles of the females for sperms. Females and males were obtained from culture bottles from which flies had been removed no earlier than two days before (*athabasca* has been found to breed no sooner than three days after emergence). Due to variation in culture bottle yields during the time of this experiment it was not considered practical to restrict the combinations always to the same numbers of flies, so the number of each sex was permitted to vary from 5 to 20 per bottle, though the ratio of females to males was always kept close to 1:1. Moreover, mortality of the flies during cohabitation caused some additional variation in the numbers of individuals. An attempt was made to use flies from as many different strains as possible from each locality, since it was expected that if any showed a radical difference from the rest, the difference would be detected and could then be investigated further. However, since there was no strikingly great difference between the results with the different strains, the results have been pooled. All combinations were made in half-pint milk bottles containing standard Drosophila food (corn meal-molasses-agar-Tegosept-yeast), the surface of the food being dusted with sawdust in the hope of preventing the flies from getting stuck. The data were accumulated from November, 1954, through February, 1955, the culture and combination bottles being kept in a room in which the temperature varied from about 17 to 24° C. (as with subsequent cultures and crosses).

Table 1 shows the pooled results of the "no-choice" combinations of Wyoming and Michigan *athabasca*. It can be seen that, although in the intralocality combinations the frequency of females found inseminated was about 75% in the Wyoming strains and 69% in the Michigan strains, none of the 233 Michigan females confined with Wyoming males was found inseminated, and only two out of the 242 Wyoming females kept with Michigan males were found with sperms in their receptacles. Adult offspring (13 females and 5 males) were recovered in one of the two culture bottles in which interlocality insemination was found. Although attempts to mate these to the parent strains and to each other were not successful, the males were found to have fully developed testes containing sperms. More than two years later (1957) this cross was confirmed by successful matings between Wyoming females with a sex-linked recessive mutant gene (bright red eyes) and Michigan males; the daughters were wild type and

sons bright-eyed, and these were fertile when mated to each other.

During this time strains of *athabasca* were obtained from Minnewaukan, North Dakota, and Cedar Lake, Ontario (near the western boundary of the province; this strain kindly furnished by Professor Th. Dobzhansky and Mr. B. Spassky), and these were employed in a few interlocality crosses. Unfortunately, both these strains were lost before they could be used extensively to study sexual isolation. Nevertheless, both North Dakota and western Ontario strains crossed rather easily with strains from Wyoming, producing numerous fertile hybrids, while neither crossed successfully with the Michigan strains employed. Moreover, as reported below (table 4), the North Dakota and western Ontario *athabasca* were found to resemble the Wyoming strains in copulation time.

D. athabasca is known to hybridize in the laboratory with the closely related species *azteca* (Sturtevant and Dobzhansky, 1936) and *affinis* and *algonquin* (Miller, 1950a). To test the crossability of the available Wyoming (and North Dakota) and Michigan strains of *athabasca* with these other species, cross combinations of these strains with stocks of *affinis* (Florida, Illinois, Nebraska, Tennessee, Texas), *algonquin* (Michigan, Nebraska), and *azteca* (California) were made in the manner already described for the intraspecific combinations. It may be seen in table 2 that, although no interspecific inseminations were found in combinations of *algonquin* and *athabasca*, interspecific inseminations were discovered in combinations of *affinis* females with both Wyoming (and North Dakota) and Michigan *athabasca* males and in all combinations of *azteca* with *athabasca* from the different localities, the frequencies of insemination varying widely from one combination to another but being regularly greater than in the combina-

TABLE 2. *Frequencies of inseminations after 10-day combinations of* D. affinis, D. algonquin, *and* D. azteca, *both intra-specific and with* D. athabasca

(The number in parentheses after each combination indicates the number of strain combinations included in the pooled data.)

Combination	Number of females	Females inseminated	
		Number	Per cent
D. affinis ♀ × *D. affinis* ♂ (6)	101	98	97
D. algonquin ♀ × *D. algonquin* ♂ (3)	106	84	72
D. azteca ♀ × *D. azteca* ♂ (2)	106	97	92
D. aff. ♀ × *D. ath.* (Mich.) ♂ (6)	121	7	6
D. aff. ♀ × *D. ath.* (Wyo. & N. D.) ♂ (8)	135	39	29
D. ath. (Mich.) ♀ × *D. aff.* ♂ (7)	104	0	0
D. ath. (Wyo. & N. D.) ♀ × *D. aff.* ♂ (4)	109	0	0
D. alg. ♀ × *D. ath.* (Mich.) ♂ (7)	101	0	0
D. alg. ♀ × *D. ath.* (Wyo. & N. D.) ♂ (9)	114	0	0
D. ath. (Mich.) ♀ × *D. alg.* ♂ (8)	107	0	0
D. ath. (Wyo. & N. D.) ♀ × *D. alg.* ♂ (9)	111	0	0
D. azt. ♀ × *D. ath.* (Mich.) ♂ (5)	109	50*	46
D. azt. ♀ × *D. ath.* (Wyo. & N. D.) ♂ (5)	100	8	8
D. ath. (Mich.) ♀ × *D. azt.* ♂ (5)	104	2	2
D. ath. (Wyo. & N. D.) ♀ × *D. azt.* ♂ (5)	108	29*	27

* Certain crosses yielded hybrids, these agreeing as to abnormalities already reported for such hybrids (Sturtevant and Dobzhansky, 1936).

TABLE 3. *Frequencies of* D. athabasca *females inseminated in three-day "choice" matings (two kinds of females with one kind of male) after seven days of ageing in isolation*

	Homogamic inseminations	Heterogamic inseminations	Chi-square	Isolation index
Wyo. ♂♂ Wyo. ♀♀, Mich. ♀♀	67/90 (74%)	3/87 (3%)	93.439	0.92
Mich. ♂♂ Mich. ♀♀, Wyo. ♀♀	68/97 (70%)	7/98 (7%)	81.068	0.82
Wyo. ♂♂ Wyo. ♀♀, N. Y. ♀♀	85/100 (85%)	35/100 (35%)	52.084	0.42
N. Y. ♂♂ N. Y. ♀♀, Wyo. ♀♀	72/100 (72%)	24/99 (24%)	46.371	0.50
Mich. ♂♂ Mich. ♀♀, N. Y. ♀♀	79/102 (77%)	1/101 (1%)	101.912	0.97
N. Y. ♂♂ N. Y. ♀♀, Mich. ♀♀	62/102 (61%)	0/101 (0%)	72.102	1.00

tions of Wyoming and Michigan *athabasca* with each other.

SEXUAL ISOLATION IN "CHOICE" COMBINATIONS OF STRAINS FROM WYOMING, MICHIGAN, AND NEW YORK

Because the sexual isolation reported here between Wyoming and Michigan *athabasca* was unexpected in view of Novitski's findings (1946), it was considered desirable to investigate the possibility of sexual isolation using strains of this species originating east of Michigan, since the eastern strains of *athabasca* used by Novitski had been obtained from Quebec, New England, New York, and North Carolina. In the summer of 1955 new *athabasca* cultures were established from collections at Cold Spring Harbor, New York.

Preliminary crosses between the New York strains and those from Michigan and Wyoming were made in October and November, 1955; these were 10–11 day "no-choice" combinations similar to those already described except that, since the New York strains were not yet well established, all combinations involved New York males (of various ages) with females of the other localities. These crosses showed that New York males would mate with both Wyoming and Michigan females. Of 132 Wyoming females kept with New York males, 55 (42%) were found inseminated. Of 82 Michigan females confined with New York males, 5 (6%) were inseminated. Moreover, both these crosses yielded fertile offspring.

Crosses were next performed in which males had their "choice" of two kinds of females. The following procedure was used. Females and males were separated within 24 hours of emergence and kept isolated in culture bottles for 6 days. They were then transferred to vials (still in isolation) and given fresh food. On the 7th day a number of males (varying from 5 to 20) were put in a culture bottle with the same or a similar number of each of two different kinds of females. Since the females from the different localities could generally not be distinguished, one kind regularly had the left wing clipped off and the other kind the right wing, the relationship as to right and left wing being reversed in about half the cases of each combination. Eight different New York strains participated in these crosses. However, due to losses

of strains during the summer of 1955, Wyoming was now represented by only one strain, Michigan by only three. Each locality combination involved several strain combinations. Cohabitations lasted from the 7th to the 10th day, on which females were dissected and their receptacles examined for sperms. Data were collected from March through July of 1956.

Table 3 shows the results of the "choice" combinations. The isolation indexes were calculated according to the method of Charles and Stalker (Stalker, 1942). It may be seen that a high degree of mating preference existed in all cases. The strongest sexual isolation was apparent between New York and Michigan. For instance, no Michigan females were inseminated by New York males, although the "no choice" combinations of the previous fall had shown some insemination in this combination, as well as fertile hybrids. The least isolation existed between Wyoming and New York. However, even in combinations of flies from these localities, there was a fairly high degree of sexual isolation. The combinations of Wyoming and Michigan gave intermediate results. It may also be seen that the frequencies of insemination between Wyoming and Michigan were much higher in these "choice" combinations than had been observed in the "no-choice" matings between strains of these localities the year before.

Observations of Mating Behavior

Mating behavior was observed in approximately one week old adults in both intra- and inter-locality combinations, the flies having been aged in isolation for six days and then put together in a clean vial on the 7th day. As reported by Miller (1951), courtship in *athabasca* differs from that of the closely related species *affinis* and *algonquin* (Miller, 1950b) in that *athabasca* males usually (though not invariably) extend and vibrate one wing rather than both wings. However, no significant differences in courtship behavior could be detected between the different strains of *athabasca*. Nevertheless, when females of one locality were combined with males of another, courtship appeared less vigorous and was much less often successful (usually unsuccessful) than in the intra-strain combinations.

Durations of copulation were determined for the existing strains of *athabasca,* as had been done earlier for older strains (lost before the present study began) from Cold Spring Harbor, New York, and Princeton, New Jersey (Miller, 1951). The prevailing temperatures during these observations varied from about 23° C. to 29° C. Nevertheless, although copulation time varied considerably in the different strains (especially the western ones), there was no obvious relationship between temperature and copulation time (such as, for example, was reported for *D. algonquin* by Miller, 1950). Consequently, the data have been pooled without regard for temperatures. The durations of copulations observed are given in table 4, which also includes data from Miller (1951). It may be seen that the durations of copulation were strikingly different between the western and eastern strains of *athabasca*. In the western strains (Wyoming, North Dakota, western Ontario) copulation time was never less than 3′ 57″, while in the eastern ones (Michigan, New Jersey, New York) copulation time never exceeded 2 minutes. Consistent with the observation of relatively long copulation in the western strains studied here is the report of Spieth (1952) that a Wyoming strain of *athabasca* (Sundance) had 5 observed copulations range from 7′ 10″ to 10′ 5″, with a mean of 7′ 45″, all well within the range of copulation times of Wyoming (and other western) *athabasca* reported here.

An attempt was made to determine durations of copulation in combinations of *athabasca* from Wyoming and New York and in descendants derived from such matings. The results of these ob-

TABLE 4. *Durations of copulation in matings of* D. athabasca *within strains from different localities (all first matings of approximately week old adults)*

(The number in parentheses after each place name indicates the number of strains contributing to the pooled data.)

Locality	Durations	Mean
Moran, Wyoming (5)	3′57″, 4′1″, 4′15″, 4′17″, 4′26″, 4′54″, 4′55″, 4′58″, 5′1″ (2), 5′2″, 5′16″, 5′19″, 5′20″, 5′25″, 5′32″, 5′38″, 5′41″, 6′0″, 6′13″, 6′14″, 6′15″, 6′27″, 6′32″, 6′41″, 7′48″, 7′56″, 8′25″, 9′54″, 11′3″, 11′36″	6′8″
Moran, Wyoming (mutant strain: "bright eyes")	4′50″, 5′29″, 6′14″, 6′35″	5′47″
Minnewaukan, N. D. (1)	6′50″, 7′27″, 7′37″, 8′25″	7′35″
Cedar Lake, Ont. (1)	4′35″, 7′16″	5′56″
Cheboygan, Mich. (6)	1′4″, 1′6″, 1′9″, 1′10″, 1′12″, 1′19″, 1′21″, 1′33″ (2), 1′34″ (3), 1′35″, 1′40″, 1′41″, 1′47″, 1′56″, 1′59″, 2′0″	1′31″
Cold Spring Harbor, N. Y., and Princeton, N. J. (1 each) (Miller, 1951)	1′12″ (2), 1′13″, 1′15″, 1′23″ (2), 1′25″ (2), 1′26″, 1′27″, 1′40″, 1′42″, 1′48″	1′25″
Cold Spring Harbor, N. Y. (5)	0′32″, 0′42″, 0′52″, 0′56″, 0′59″, 1′6″, 1′9″, 1′17″, 1′25″, 1′46″	1′11″

servations are given in table 5. Though the results are rather meager, especially for certain combinations (due to difficulties in getting matings and in getting hybrids between Wyoming females and New York males), they suggest something concerning the basis for the difference of copulation times between the Wyoming and New York strains. The few interlocality matings suggest that copulation time is determined by the male, such as has been reported in certain other species, for example, *D. subobscura* (Milani, 1952). The matings of F_1 females and males and of F_1 males with parent strain females had durations that extended well into the time zone that separated the durations observed for the Wyoming and New York strains—i.e., from 2′ to 3′ 57″. A few facts point to an influence of the male partner's X-chromosome on copulation time. The few copulations observed between F_1 females and males of the Wyoming female by New York male cross were all longer in duration than any observed involving F_1 males of the reciprocal cross. Moreover, F_2 males that had received the sex-linked recessive mutant gene for bright eyes from Wyoming males mated to New York females (and, consequently, must have had at least part of a Wyoming X-chromosome) had matings that were generally longer than those involving wild-type F_2 males (with New York X-chromosome material) from the same crosses.

CROSSABILITY AND MATING BEHAVIOR OF NEW STRAINS FROM WISCONSIN, MICHIGAN, ONTARIO, AND QUEBEC

During the summer of 1956 collections by the author in southern Ontario (Al-

gonquin Park) and Quebec (Gatineau Park, Ste. Anne de Bellevue, Laurentides Park) made possible the establishment of new strains of *athabasca* from these places. Also, Dr. H. D. Stalker of Washington University kindly made available *athabasca* from his collections in northern Wisconsin (Iron River) and Michigan (Iron Mountain), from which new strains were derived. Although these stocks have not yet been used in sexual isolation experiments such as those already described, attempts to hybridize the new strains with the old ones from Wyoming, Michigan (U.M.B.S.), and New York (all possible combinations of new localities with old ones having been attempted) have given difficulties suggestive of such isolation. So far only the following crosses have yielded hybrids (all of which were fertile): Wyoming females by Iron River males; Iron Mountain females by U.M.B.S. males; Wyoming females by Algonquin Park males, both reciprocal crosses of Algonquin Park by U.M.B.S.; both reciprocal crosses of Gatineau Park by U.M.B.S.: both reciprocal crosses of Ste. Anne de Bellevue by U.M.B.S.; and Wyoming females by Laurentides Park males.

Table 6 shows durations of copulation observed in the recently established strains of *athabasca*. Although the small numbers of observations afford little basis for comparing these strains with each other or with the older ones, it may be seen that the long copulation time characteristic extends into the east, being especially prominent in the easternmost strains (Laurentides Park), and that some strains expressed both long and short copulation times (in particular, certain ones from Iron Mountain and Gatineau Park).

TABLE 5. *Durations of copulation in mating combinations of Wyoming and New York* D. athabasca *(one strain from each locality) and of their descendants (all first matings of approximately one week old adults)*

Combination	Durations	Mean
Wyo. ♀♀ × N. Y. ♂♂	1′3″, 1′11″	1′7″
N. Y. ♀♀ × Wyo. ♂♂	3′55″, 4′18″, 6′49″, 6′56″	4′29″
F_1 (Wyo. ♀ × N. Y. ♂) ♀♀ × ♂♂	3′14″, 3′21″, 5′19″	3′59″
F_1 (N. Y. ♀ × Wyo. ♂) ♀♀ × ♂♂	1′9″, 1′13″, 1′16″, 1′18″, 1′21″, 1′49″, 1′58″, 2′2″ (2), 2′16″, 2′25″, 2′26″, 2′38″, 2′50″, 3′9″	1′59″
Wyo. ♀ × F_1 (N. Y. ♀ × Wyo. ♂)♂	1′27″, 2′6″, 2′29″	2′1″
N. Y. ♀ × F_1 (N. Y. ♀ × Wyo. ♂)♂	2′30″, 2′36″	2′33″
F_2 (N. Y. ♀ × Wyo. br.* ♂) F_2 ♀♀ × "wild" F_2 ♂♂	0′14″, 1′29″, 1′34″, 1′42″, 2′3″ (2), 2′28″, 2′39″, 2′55″	1′54″
Wyo. ♀ × F_2 (N. Y. ♀ × Wyo. br. ♂) "wild" F_2 ♂♂	2′3″	2′3″
N. Y. ♀ × F_2 (N. Y. ♀ × Wyo. br. ♂) "wild" F_2 ♂♂	2′9″, 2′30″	2′20″
F_2 (N. Y. ♀ × Wyo. br. ♂) F_2 ♀♀ × "bright" F_2 ♂♂	2′46″, 3′29″, 5′15″	3′50″
Wyo. ♀ × F_2 (N. Y. ♀ × Wyo. br. ♂) "bright" F_2 ♂♂	3′54″	3′54″

* "br." signifies "bright eyes," a sex-linked recessive mutant derivative of Wyoming strain.

TABLE 6. *Durations of copulation in matings of* D. athabasca *within strains from different localities (all first matings of approximately week old adults)*

Strains established in 1956. The number in parentheses after each place name indicates the number of strains contributing to the pooled data.

Locality	Durations	Mean
Iron River, Wisconsin (1)	4′56″, 5′49″, 7′34″	6′7″
Iron Mountain, Michigan (2)	1′25″, 1′26″, 2′8″, 4′12″, 5′27″	2′56″
Algonquin Park, Ontario (2)	1′17″, 1′30″, 1′34″, 1′35″, 1′39″, 1′44″, 1′45″, 2′16″, 2′42″	1′47″
Gatineau Park, Quebec (5)	1′11″, 1′24″ (2), 1′26″, 1′41″, 1′56″, 1′59″ (2), 2′32″, 4′11″ (2)	2′10″
Ste. Anne de Bellevue, Quebec (5)	1′20″, 1′35″, 1′38″, 1′58″, 2′2″, 2′4″, 2′21″	1′51″
Laurentides Park, Quebec (3)	5′56″, 7′18″, 7′20″, 7′59″, 10′7″, 11′44″, 20′56″	10′11″

DISCUSSION

There are now numerous reports of intraspecific sexual isolation between laboratory strains of *Drosophila* species. Such isolation was reported by Dobzhansky and Koller (1938) between strains of *D. miranda* from California and the state of Washington; by Stalker (1942) between different Ohio strains of *D. americana;* by Dobzhansky (1944) between Mexican and Brazilian *D. sturtevanti;* and by Dobzhansky and Streisinger (1944) (as well as Levene and Dobzhansky, 1945) between strains of *D. prosaltans* from Brazil, Guatemala, and Mexico. Various degrees of intraspecific sexual isolation have been reported, with isolation indexes as high as 0.95 (*D. prosaltans* Brazilian males with Brazilian and Mexican females; Levene and Dobzhansky, 1945). Some negative isolation indexes have been reported (indicating "preference" of males for alien females), as in certain combinations of Brazilian *D. prosaltans* males with Mexican and Brazilian females (Dobzhansky and Streisinger, 1944). The degree of isolation has been found to vary widely with different strains of the same species, the extent of isolation not strictly correlated with geographical origin, as, for example, reported for *D. sturtevanti* (Dobzhansky, 1944), in which strains from remote localities sometimes showed less isolation than did those from less remote localities.

The sexual isolation data presented here for the *D. athabasca* strains from Wyoming, Michigan, and New York show no essentially different features from those already reported for the other species, though they do establish a rather high degree of isolation within this North American species. The failure of Novitski (1946) to find sexual isolation between his eastern and western strains of *athabasca* suggests that those older strains of this species were much less isolated from each other than were the Wyoming, Michigan, and New York strains on which this report is based.

A high degree of sexual isolation may be taken along with other evidence as a basis for the recognition of sibling species. For example, Dobzhansky (1946) recognized the distinctness of the Brazilian species *D. equinoxialis* from *D. willistoni* on the basis of an almost complete failure of insemination to take place between them in the laboratory. Moreover, no hybrids were detected in the few culture bottles in which insemination had occurred. Though there was a significant (though overlapping) size differ-

ence between these two forms, no reliable morphological criterion for separating individuals of these species was available until Spieth (1949) discovered an internal characteristic (spermatheca tube shape) which differentiated them.

Despite the high interlocality sexual isolation reported here within *D. athabasca,* the available evidence appears as yet insufficient to serve as a basis for subdividing the species into taxonomic categories. In particular, though a very high degree of sexual isolation separates the Michigan strains from the Wyoming and New York strains, some matings of Michigan with the other strains (Wyoming females by Michigan males, Michigan females by New York males) has been found to yield normal, fertile hybrids. Moreover, no clearly recognizable morphological or physiological characteristic has been found to distinguish the strains of the different localities. Although the New York *athabasca* often appeared paler than those from Wyoming and Michigan, this was not always the case and did not afford complete separation from the others. Moreover, the strongly isolated Wyoming and Michigan strains showed no such color difference. Although variation in copulation time serves to distinguish the Wyoming (and other western) strains of *athabasca* from those from Michigan and New York, it does not do so for the strongly isolated Michigan and New York strains. Moreover, observations of matings in new strains from Michigan, Ontario, and Quebec show that some eastern *athabasca* possess the long copulation trait previously found only in the western strains.

In conclusion, it appears that the strains of *athabasca* studied here must represent populations that have undergone a certain amount of genetic divergence concerning mating propensity and behavior. However, the evidence is not yet sufficient to show very well the pattern of this divergence. Additional information is needed on *athabasca* from localities other than those studied here, and work to obtain this information is in progress.

Summary

Several geographically different strains of *D. athabasca* were studied as to sexual isolation and mating behavior. Strains from Wyoming and Michigan showed a marked degree of sexual isolation, though rare matings between Wyoming females and Michigan males did yield fertile hybrids. Strains from New York likewise were strongly isolated from Michigan strains, but some fertile hybrids were obtained between Michigan females and New York males. Wyoming and New York *athabasca* showed some isolation but crossed much more easily in both reciprocal directions than either did with Michigan, producing fully fertile hybrids. The duration of copulation was found to be long (about 4′ or more) in western strains of *athabasca* (Wyoming, North Dakota, western Ontario), short (2′ or less) in certain eastern strains (Michigan, New Jersey, New York), while other eastern strains (Michigan, Ontario, Quebec) had either a mixture of short and long matings or exclusively long ones (Quebec). Intermediate mating times were observed in the descendents of Wyoming (long) and New York (short) strains.

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HYBRIDIZATION IN SOME SPECIES OF *PTERIS* L.

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INTRODUCTION

Pteris L. is an almost exclusively tropical genus of ferns of some 280 species (Copeland, 1947), many of which are distinctive and somewhat isolated. Also included in the genus, however, are several complexes containing from a few to many species. These present great taxonomic difficulties and the interrelationships of the components can often only be deduced by experimental methods. One such complex is centered on *P. quadriaurita* Retz. and the present paper deals with the behavior in Ceylon of three species of this group.

Cytotaxonomic studies carried out over the last five years (Walker, 1956; Walker, publication pending) have shown that this complex contains many separate species which are superficially very much alike. Differences nevertheless exist in such fundamental characters as the level of polyploidy, type of breeding system, features of the spores and details of the juvenile plants. These differences, once determined by experimental methods, can then be correlated with relatively small but constant features on dried specimens, enabling species to be recognized in herbaria with, at most, the aid of a pocket lens.

At least seven species of the *P. quadriaurita* complex are to be found growing in Ceylon, including *P. quadriaurita* Retz. *sensu stricto* itself. Several are ecologically or genetically isolated from one another and remain distinct in nature, but the three to be discussed below have hybridized freely resulting in the formation of very conspicuous hybrid swarms. Such hybrid swarms may continue to segregate and back-cross or, under certain circumstances, may become stabilized as a result of the sexual breeding system being replaced by apogamy. A complex situation of this nature has led to taxonomic difficulties even greater than those already inherent in the group as a whole.

MATERIALS AND METHODS

In 1951 an expedition headed by Professor I. Manton went to Ceylon from the Botany Department of Leeds University, England. The primary purpose of the expedition was to collect material for a cytological survey of the Pteridophyte flora of the island (Manton, 1953) and numerous living plants and herbarium specimens of *Pteris* were turned over to me for cytotaxonomic investigation after only a few preliminary chromosome counts had been made (Manton and Sledge, 1954).

This material has since been considerably augmented as a result of a visit to Ceylon in 1954 by the author in company with Dr. Sledge and by generous gifts from correspondents in Asia, Africa and Australasia. These gifts included some 60–70 species of *Pteris* all of which have been studied alive though only a few will be referred to here.

For each species, adult plants have been raised from spores in order to study the complete life cycle. Most of them proved easy to grow in a heated greenhouse at an average temperature of 60–80° F, provided they were not overwatered. As a routine practice, spore mounts were made in glycerine jelly for a detailed microscopic examination, prothalli were examined to determine the type of breeding system (sexual vs. apogamous), characteristics of the juve-

nile plants were noted, and finally both meiotic and mitotic chromosomes were examined by the use of aceto-carmine squashes. In addition many interspecific hybrids have been made and cytologically analysed to give data on the interrelationships of the species. The technical methods involved in these processes are standard (cf. Manton, 1950; Walker, S. 1955, etc.).

A Brief Taxonomic History of the *P. quadriaurita* Complex

The type species of the complex, *P. quadriaurita* Retz. *sensu stricto* was named and described in 1791 by Retzius. It was based on a specimen collected in Ceylon by König. This species in the strict sense is confined to Ceylon and Southern India but the name has been applied by numerous authors to many plants from almost the entire range of the genus. Hooker (1858) in particular placed a very liberal interpretation on the name, whilst Hieronymus (1911 and 1914) described a large number of new species from Africa and Asia which, however, he regarded as being closely allied to *P. quadriaurita.*

In Ceylon the situation is complicated by the existence of a large number of problematical forms which are difficult to fit into any specific category. One particularly common form characterized by the abortion of several pinnules was figured by Beddome (1873) under the name of *P. Otaria* and yet another with its pinnules represented by small lumps was figured and labelled "*P. Otaria* var.?" A few years later (1883) Beddome quoted both illustrations under the name of *P. quadriaurita* var. *ludens.* As Beddome regarded *P. Otaria* and *P. quadriaurita* var. *ludens* as synonymous the term *P. Otaria* will be used throughout this paper for the sake of brevity.

Hieronymus (1914) redescribed *P. quadriaurita* with a wealth of detail and included in his description and citations some forms which showed a small amount of the abortion of the pinnules so characteristic of *P. Otaria* and concluded that *P. Otaria* was not worthy of taxonomic recognition and was in his opinion possibly a common mutation.

Giesenhagen (1918) on the other hand, illustrated a series of fronds characterised by varying degrees of abortion of the pinnules, and after considering Thwaite's suggestion (1864) that some of the forms were of hybrid origin, concluded that all of these including *P. Otaria,* represented developmental stages such as are well known in some ferns, e.g., *Polypodium Phymatodes* L. He suggested that the abortion of the pinnules depended upon the lack of availability of nutrients to the young fronds and was not genetically determined.

Demonstration of the Hybrid Nature of *P. Otaria*

The Ceylon expedition was faced with a bewildering array of plants of *Pteris,* many of which could not be named and amongst these, specimens more or less resembling *P. Otaria* occupied a central position (cf. Text-fig. 1, b-g). It seemed to be crucial therefore to investigate the status of *P. Otaria* and to determine whether or not it was a valid true-breeding species or if the whole situation was being complicated by hybridity or some other cause.

Living plants of *P. Otaria* had been examined cytologically (Manton and Sledge, 1954; Walker, 1956) and found to be diploid ($2n = 58$) and sexual. Following a perfectly regular meiosis nearly 100% of well-filled viable spores were produced in all such plants. Spores were collected from one of these plants selected for its close resemblance to Beddome's illustration and sown. The prothalli so obtained were allowed to self-fertilize and a small population of sporophytes was raised under uniform conditions. The individuals of this population varied considerably in the outline of the fronds as shown in figure 2, ranging from plants

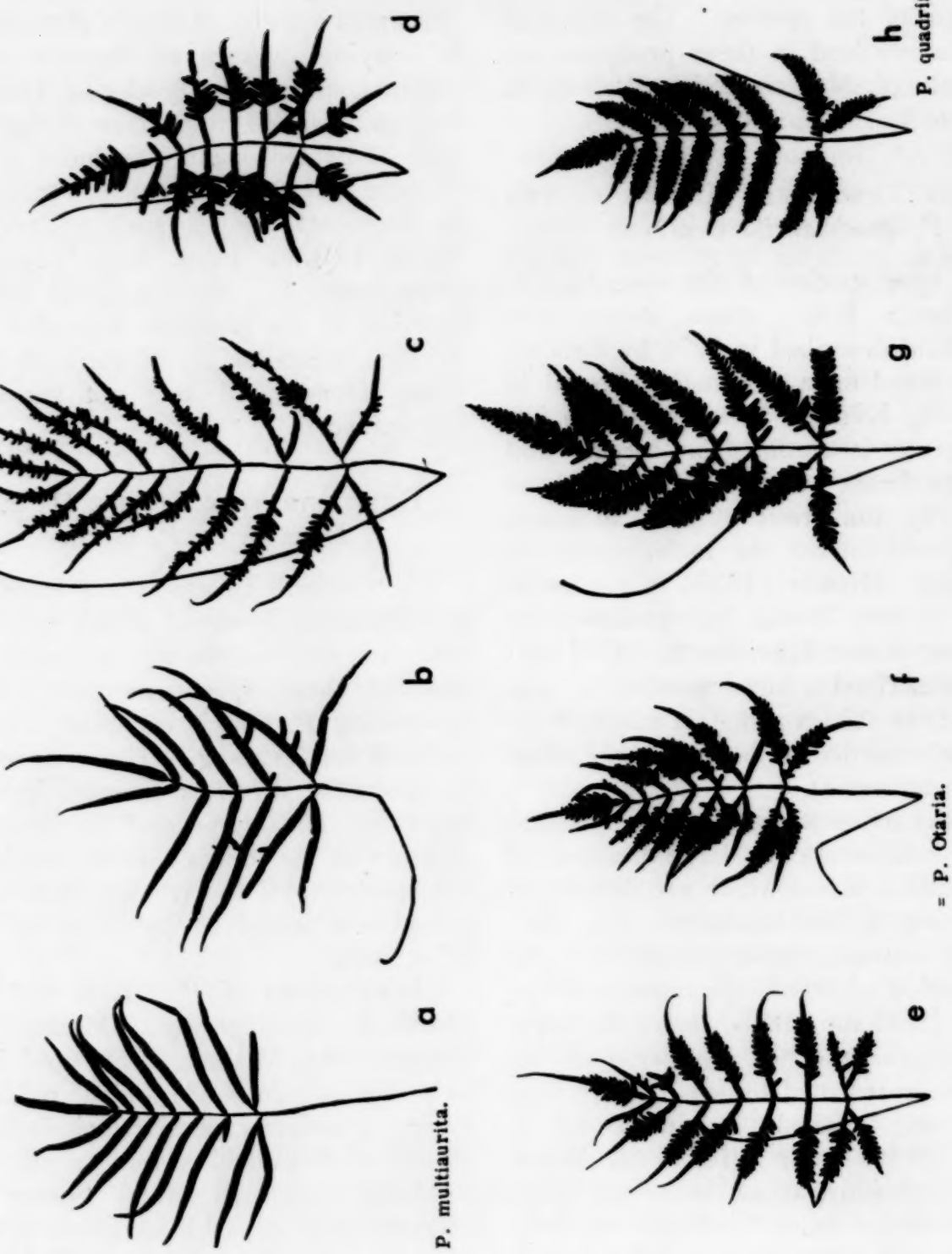

FIG. 1. Silhouettes of some fertile adult fronds of the *P. multiaurita-P. quadriaurita* hybrid swarm collected in Ceylon. × ⅛.

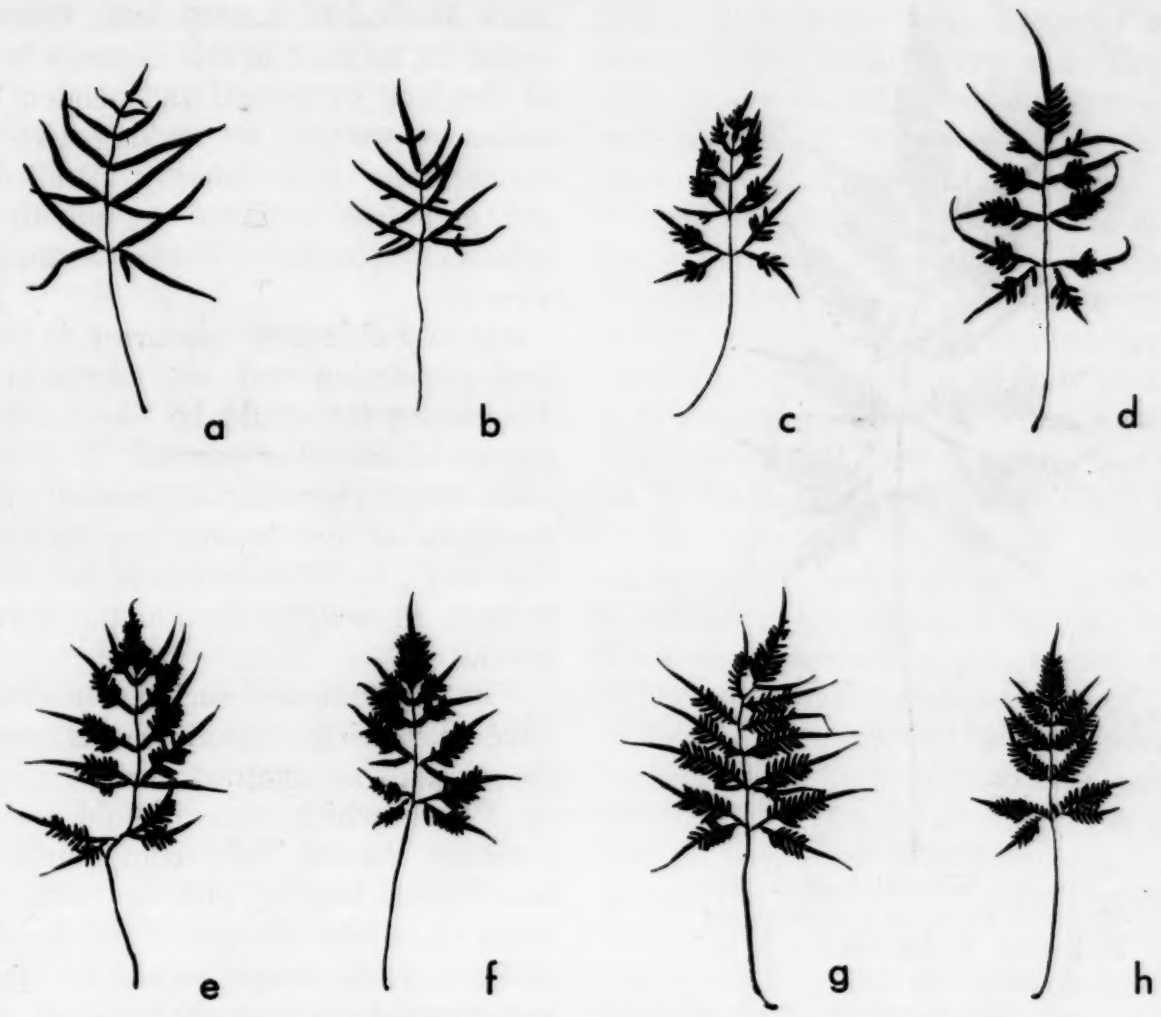

FIG. 2. Silhouettes of fertile adult fronds of the progeny of self-fertilized *P. Otaria*. × 1/8.

with simply pinnate fronds to some with completely compoundly pinnate fronds. Between these two extremes there were many degrees of intermediates, among which the parental *P. Otaria* was represented several times (fig. 2, e-f). All the plants of the population were diploid and sexual and set about 100% well-filled viable spores following a regular meiosis. This experiment was repeated several times, using different plants of *P. Otaria* as the source of spores for raising populations, and each time with the same result.

The conclusion drawn from these experiments is that *P. Otaria* is not a valid species but is really a particularly common member of a hybrid swarm which had been given a specific name and whose hybrid nature was shown on self-fertilization by the complicated segregation for frond outline.

RESYNTHESIS OF *P. Otaria*

The problem remained of determining the species involved in the formation of this hybrid. It appeared probable from the range of frond outline among the segregating progeny (fig. 2, a-h) that a simply pinnate species had hybridized with a fully compoundly pinnate species. The only two simply pinnate species in Ceylon that could be considered in the rôle of one parent were *P. ensiformis* Burm. and *P. multiaurita* Ag. Both of these had been found by the Ceylon expedition and were available alive.

Thwaites (1864) had tentatively suggested that *P. ensiformis* might be involved but the cytology showed this to be extremely improbable as this species is tetraploid ($2n = 116$) in contrast to the diploid hybrid. Further, when *P. ensiformis* was crossed with *P. Otaria,* sterile, triploid hybrids resulted showing com-

FIG. 3. Silhouette of a fertile adult frond of a synthesised F_1 hybrid, *P. multiaurita* × *P. quadriaurita*. × 1/8.

plete failure of pairing of the chromosomes at meiosis.

P. multiaurita, however, proved to be a diploid sexual species and furthermore agreed perfectly with the simplest form obtained from the segregating *P. Otaria* population (fig. 2, a) not only in gross morphology but also in such critical characters as spore detail, and the juvenile stages. Thus it was virtually certain that *P. Otaria* was a hybrid involving *P. multiaurita* as one of its parents. This was confirmed by crossing *P. Otaria* and *P. multiaurita,* resulting in the formation of hybrids showing complete pairing of the chromosomes at meiosis and the production of viable spores.

Anderson, in a long series of papers (see especially, Anderson 1949) has demonstrated that if members of a hybrid swarm are available for study and one of the parents is known the characters of the unknown parent may be deduced, leading to its identification. Unfortunately such elegant techniques as Anderson's Method of Extrapolated Correlates could not be used in this instance because of the lack of several independent variables. However, by making two basic assumptions a sufficiently detailed description was obtained to identify the unknown parent. These assumptions were:

1) Any character appearing in the hybrid population and not represented in *P. multiaurita* would be due to the influence of the other parent.

2) Any character appearing in all members of the hybrid population and also in *P. multiaurita* would be common to both *P. multiaurita* and the unknown parent.

The application of such a crude method gave surprisingly good results and the descriptions so obtained were of a species of *Pteris* which was diploid, sexually breeding, having fully compoundly pinnate fronds bearing pinnules with a serrated tip, whilst the spores and the details of the juvenile stages would be virtually indistinguishable from those of *P. multiaurita.*

No plant answering to this description had been found by the 1951 expedition but the present writer found plants growing in abundance in restricted areas in Ceylon in 1954 which tallied perfectly with the predictions made above. Living plants and herbarium specimens were sent to England and later an opportunity arose of examining the type specimen of *P. quadriaurita* Retz. *sensu stricto* from the Retzius Herbarium in Lund. The specimens gathered in 1954 agreed exactly with the type specimen and can be referred with confidence to this species.

Thus it appeared most likely that *P. Otaria* was one member of a hybrid swarm produced as a result of the crossing of *P. multiaurita* and *P. quadriaurita* s.s. This hypothesis has now been fully confirmed by experimentally crossing *P. multiaurita* and *P. quadriaurita.* The F_1 hybrids as shown in figure 3 are morphologically much closer to *P. quadriaurita* than to *P. multiaurita* but the F_2 genera-

tion which has been raised from them has segregated to give a series of forms ranging from one parental extreme to the other and in which *P. Otaria* is represented several times. This F_2 population completely duplicates the populations previously raised as a result of self-fertilizing *P. Otaria*.

In Ceylon a large number of wild specimens of the hybrid swarm almost exactly matching those raised in cultivation were collected by the author and a few are shown in figure 1. Many more intermediate frond types were found than are illustrated and it is evident that multiple factors are involved, leading to a complicated segregation. *P. Otaria* is not therefore merely the expression of the heterozygous condition of one or two genes.

Field Observations on *P. quadriaurita*, *P. multiaurita* and their Hybrid Swarms

P. quadriaurita grows in great numbers at several localities in Ceylon but is restricted to such parts of the large virgin forests which are on the wetter fringe of the Dry Zone. Such forests do not cast a very intense shade and in contrast with those of wetter areas have a very sparse ground flora. *P. multiaurita* grows over much of the area in Ceylon suitable for the growth of ferns but according to the writer's observations is to be found only as small populations, typically of a few dozen plants or less. This species tends to favour habitats that are lightly shaded such as at the edge of forests or where herbaceous plants or shrubs afford some protection from the strong light without casting a dense shade. Thus *P. quadriaurita* is numerous in individuals at any particular locality but such localities are very restricted in area and distribution, contrasting strongly with *P. multiaurita* which is sparse in individuals but has a wide distribution in Ceylon.

Where these two species have met in the past hybrid swarms occur in great profusion. Such swarms are very spectacular both in the large numbers of individuals and in their very wide distribution in the island. So numerous and well-established are these hybrids and their segregants that it is probably no exaggeration to say that they are among the commonest of any fern in Ceylon. Roadside banks, paths through forest and similar examples of disturbed ground form the typical habitat of these plants.

It would appear from a study of such populations that once a hybrid has been established in a particular area it is capable of rapidly colonizing the area with its segregants and most populations show a complete spectrum of forms passing from one parental type to the other. Where such hybrids meet the large populations of *P. quadriaurita* of the forests, back-crossing evidently occurs since on the fringes of the forest numerous plants are to be found which approach very closely the form of the pure species and only a few approach *P. multiaurita* in morphology. Such back-cross types are very rapidly replaced by the pure *P. quadriaurita* only a few yards in from the forest edge, except where broad paths penetrate the forest.

Since *P. multiaurita* and *P. quadriaurita* can be hybridized in cultivation with the greatest of ease it appears that the two species are separated in nature by ecological barriers only. In the case of ferns (where there is a well-marked alternation of generations) ecological factors may play an important part in the life of either the prothallus or the sporophyte (or both). Sporophytes of both these species and members of their hybrid swarms have been grown in the tropical greenhouses at Leeds under uniform conditions of temperature, soil, moisture, lighting, and humidity, and they have not noticeably differed in their reactions to these factors. On the other hand it was noticed when raising prothalli under uniform conditions that these differed in the vigor of their growth and after experimenting a little it was found that satisfactory growth was dependent

on the degree of shading received. Thus the prothalli of *P. multiaurita* grew most vigorously in lightly shaded conditions and not so well in either full light or heavy shade, whilst those of the hybrid swarm were only vigorous in well-lighted conditions and rapidly declined in vigor and eventually died as the amount of shading was increased. These reactions of the prothalli to light are of interest as there is a striking correlation with the conditions under which the plants grow in nature, *P. multiaurita* growing in lightly shaded places such as the edge of forests, etc., as has been noted previously, whilst the hybrid swarms grow on disturbed ground—a habitat which is typically well-lighted.

Prothalli of *P. quadriaurita* showed a very high tolerance to a large range of lighting conditions and exhibited in cultivation little difference in vigor when grown in full light or dense shade, suggesting that ecological factors operate here not on the prothalli as in the other two instances quoted but on the sporophyte. The bareness of the forest floor in localities where this species grows suggests that freedom from competition from other plants may be of importance here.

It seems likely, therefore, that *P. multiaurita* and *P. quadriaurita* are ecologically separated by the two factors of light and competition, the former factor operating at the prothallial stage of *P. multiaurita* and limiting this species to habitats which are lightly shaded, whilst the latter factor is important in the sporophytic stage of *P. quadriaurita,* limiting this species to habitats in which there is freedom from competition from other low-growing plants. Where one habitat abuts onto the other, as at the edge of the Dry Zone forests, hybrids are formed and these fertile sexual hybrids and their segregants can colonise almost any area of ground which is sufficiently well-lighted to enable the prothalli to grow. The past history of the hybrid swarms must no doubt remain a matter for conjecture but it is difficult to resist the suggestion that their incidence is likely to have been greatly increased by disturbances associated with the sudden and spectacular opening up of the country by new roads, and by the felling of large areas of forest in the wetter parts of the Island to make way for the establishment of large coffee and, later, tea estates during the past one and a half centuries.

A Further Complication

A third member of the *P. quadriaurita* complex in Ceylon is a species known as *P. confusa* T. G. Walker (Walker, publication pending). This is diploid ($2n = 58$) and apogamous and has a fairly wide distribution in the wetter parts of the Island. In common with other apogamous ferns this species produces prothalli which, whilst lacking functional archegonia, do produce numerous antheridia releasing perfectly normal spermatozoids. In consequence such prothalli can be used in hybridization experiments as male parents provided that prothalli of a sexual species are used as the female parents. In this way hybrids have been raised in cultivation between *P. confusa* on the one hand and *P. quadriaurita, P. multiaurita* and several members of the *P. quadriaurita* × *P. multiaurita* hybrid swarm on the other hand. Such hybrids are triploid since, although both the parent sporophytes are diploid the male gametes of the apogamous species are unreduced in chromosome number.[1]

These triploid hybrids have a somewhat reduced proportion of viable spores which, however, inherit the apogamous mechanism and this has two important consequences:

1) The hybrids are fertile, since the viable spores give rise to apogamous prothalli.
2) Due to the loss of the sexual mechanism the hybrids do not segregate and hence breed true indefinitely.

[1] The reader who is unfamiliar with the cytological mechanism of apogamous ferns is recommended to read Manton (1950), Chapter 10.

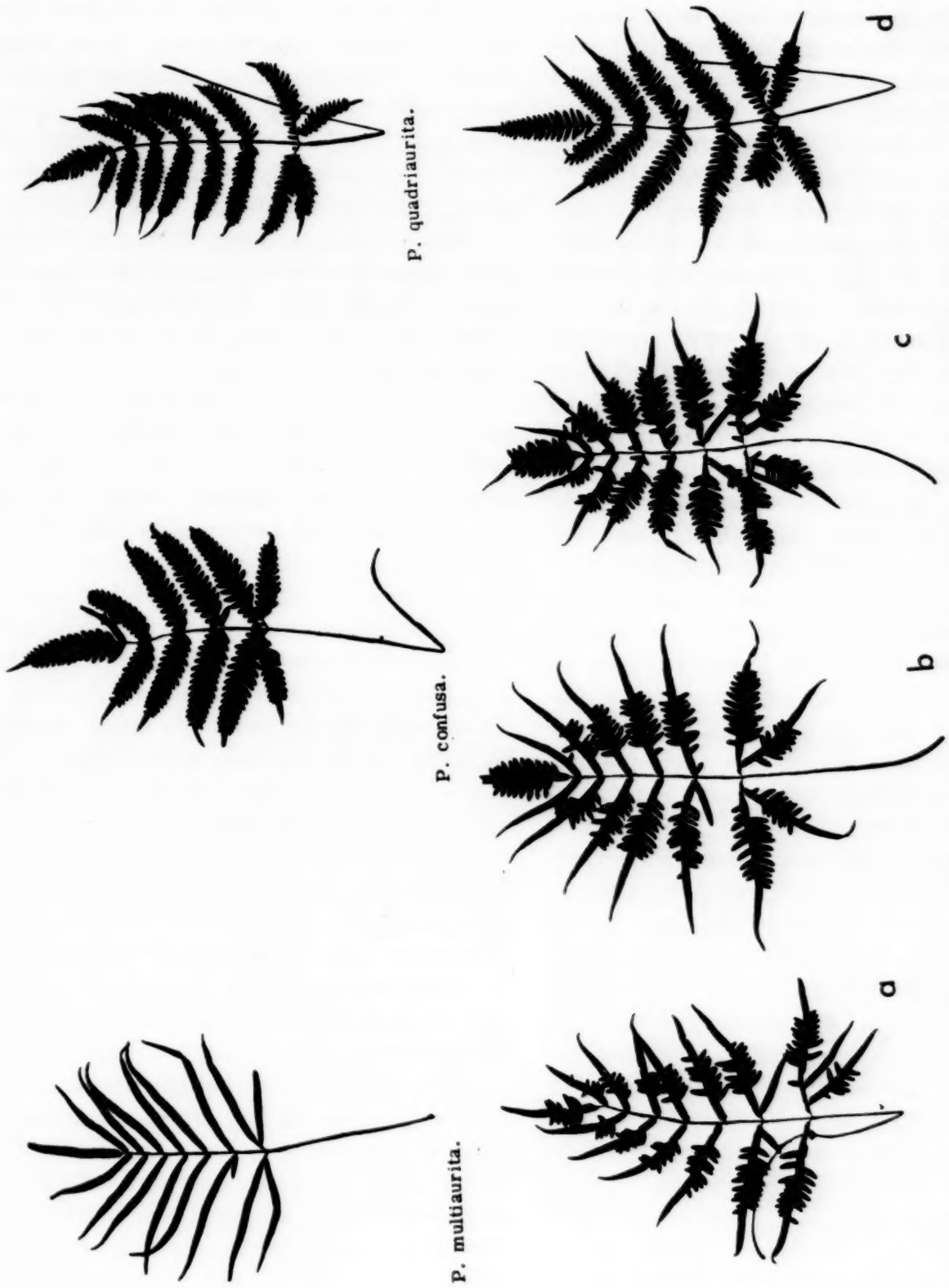

FIG. 4. Top row: silhouettes of fertile adult fronds of the parental species, *P. multiaurita*, *P. confusa*, *P. quadriaurita*. Lower row: silhouettes of comparable fronds of synthesised triploid apogamous hybrids. a). *P. multiaurita* × *P. confusa*. b). (*P. multiaurita* × *P. quadriaurita*) × *P. confusa*. c). (*P. multiaurita* × *P. quadriaurita*) × *P. confusa*. d). *P. quadriaurita* × *P. confusa*. All × ⅛.

A series of four fronds has been selected and illustrated in figure 4, a-d, showing the range of frond outlines that are produced. If this illustration is compared with figure 1 it will be apparent how closely these triploid hybrids conform in outline to the last 4 or 5 members of the diploid sexual hybrid swarm shown. The simpler members of the series are, however, not duplicated.

Such experimentally produced triploid hybrids are not purely of theoretical interest since wild hybrids of this parentage have been found growing in Ceylon by the writer though as yet only as single plants. In the Catchment Area of Kandy at the top of Mottana-Pottana, hybrid swarms of *P. quadriaurita-P. multiaurita* origin may be found growing interspersed with *P. confusa* and occasional triploid hybrids of the type illustrated in figure 4 may be found. This area has been radically altered in character in little more than a century, having been originally thick forest which was then cut down to make way for a tea estate. At the beginning of the present century the tea estate was abandoned and then planted with trees which have now grown to a great height, restoring the original forest conditions in a modified form (T. B. Worthington, personal communication). Such violent alterations in the character of the habitat suggests that these triploid hybrids are of very recent origin and have been formed in the last phase of these changes. It would be interesting to see if over the course of the next few decades these fertile hybrids will build up into large populations.

Discussion

The taxonomic confusion caused by the hybridization of *P. quadriaurita* and *P. multiaurita* has been great especially since the descendants of such hybrids are often commoner than either parent. This confusion has resulted in the giving of such names as *P. Otaria* and *P. quadriaurita* var. *ludens* to what are now known to be nothing more than morphologically conspicuous segregants of hybrid swarms. This could not have been worked out from herbarium studies alone, still less could the true nature of the triploid hybrids stabilized by apogamy have been deduced without the application of experimental methods.

It can now be recommended that in the Ceylon flora any fern having a morphology falling within the range included by figure 1, b-g and figure 4, a-d should be designated as a hybrid and that specific names should only be retained for *P. multiaurita* (fig. 4a), *P. quadriaurita* (fig. 4c) and *P. confusa* (fig. 4b).

If it is desired to distinguish between sexual (fig. 1, b-g) and apogamous hybrids (fig. 4, a-d) this can be done by reference to the spores. The diploid sexual hybrids all have nearly 100% well filled light brown spores which are about 30μ in diameter whilst the triploid apogamous hybrids have spores of which only at most 40%, and usually far less, are well-filled, dark brown, and very large, the remaining percentage being small, shrivelled and obviously non-viable.

The retention of separate specific names for *P. multiaurita* and *P. quadriaurita* is not necessarily disturbed by the fact that the two species have the close relationship of ecotypes. There is ample precedent for the taxonomic recognition of ecotypes as species in suitable cases and when it is convenient to do so (e.g., *Melandrium rubrum* and *album* Baker (1948), *Coprosma propinqua* and *robusta* (Allan, 1929), *Salvia apiana* and *mellifera* (Anderson and Anderson, 1954) etc., etc.). In the genus *Pteris* there are many unrelated species which show a deceptive morphological resemblance but which must necessarily be treated as separate. In *P. quadriaurita* and *P. multiaurita* on the other hand the morphological differences are so extreme that it is certainly a matter of herbarium convenience to name them separately.

A word of warning is, however, necessary about the continued uncritical use

of the name *P. quadriaurita sens. lat.* for plants from regions outside the restricted area of southern India and Ceylon in which *P. quadriaurita* Retz. *sens. strict.* is known to occur. Several such plants have been received from collectors in Africa and Australia, some of which have been investigated experimentally in a preliminary way with very diverse results. Thus a West African plant when crossed with *P. multiaurita* from Ceylon formed vigorous hybrids quite readily but at meiosis these hybrids showed only partial chromosome homology and were sterile. Another plant from Australia would not hybridise with *P. multiaurita* at all. It is therefore recommended that the name *P. quadriaurita* should not in future be used in any sense other than that of Retzius *sens. strict.* and that other names should be found for the very numerous superficially similar species in other parts of the world.

Apart from these taxonomic implications the evolutionary situation revealed within the complex in Ceylon is of unusual interest. Thus the emergence of *P. quadriaurita* and *P. multiaurita* as either separate ecotypes or separate species is the first case in ferns in which a wholly genetical evolutionary mechanism has been detected in action uncomplicated by polyploidy and not yet involving disturbance to chromosome homology. Their divergence is certainly recent in terms of relative fern chronology since this divergence, though considerable, affects only a few characters and the geographical range is small. Recent human interference in Ceylon has broken through the ecological barriers separating them and hybrid swarms have resulted. Continued destruction of the natural habitats in the future could lead to local extinction of the more sensitive of the two, namely *P. quadriaurita.* In such a case one might expect that one or more new forms adapted to the new environmental conditions might become stabilized from the descendants of hybrids.

The apogamous hybrids with *P. confusa,* which have certainly been formed during the last half century or so, are of interest as an example of how triploid apogamous populations indistinguishable from species could arise. At present such hybrids are sporadic in occurrence but they are very vigorous and have a high spore output in spite of the reduced percentage of viable spores and there seems no reason why true breeding and abundant local populations should not be produced from them in time. Whether or not this will occur in any particular case cannot be predicted in advance since it will depend on local opportunity as well as on adaptive vigour and reproductive capacity. We know, however, that something comparable to this has happened many times in nature since apogamous fern species are more commonly triploid than any other ploidy.

It is evident that the whole *P. quadriaurita* complex is unstable and is still in a state of active change in which continued speciation and evolution can be expected.

Summary

Three species of the *Pteris quadriaurita* complex of ferns in Ceylon have been studied cytotaxonomically. These are *P. quadriaurita* Retz. *sensu stricto, P. multiaurita* Ag., *P. confusa* T. G. Walker. It has been found that *P. quadriaurita* s. s. and *P. multiaurita* have marked ecological preferences and both are diploid and sexual. Where the natural habitat has been disturbed by man these two species frequently hybridize and vast hybrid swarms showing a complicated segregation are formed. Some of these segregants have been given names by taxonomists, notably *P. Otaria* and *P. quadriaurita* var. *ludens* but their heterozygous condition in nature has been clearly demonstrated by breeding from them and they have also been resynthesised from the parental species.

P. quadriaurita and *P. multiaurita* have diverged relatively recently and this is the first analysis to be made in the ferns

which has involved speciation depending on genetic change alone without involving loss of chromosome homology or polyploidy.

P. quadriaurita, P. multiaurita or their hybrids cross with *P. confusa,* a diploid apogamous species to produce triploid apogamous hybrids which breed true. Such di- or tri-hybrids are so distinctive morphologically that if their history had not been known they could well have been given specific names. This may be necessary in the future if homogeneous populations become established from sporadic individuals which exist at present.

It is evident that the *P. quadriaurita* complex as a whole has not become fully stabilized and continued evolution and speciation is to be expected.

Acknowledgments

The writer is indebted to the Agricultural Research Council, to the Scholarships Committee and to the Priestley Fund of Leeds University for grants which made possible his visit to Ceylon; to Mr. A. H. G. Alston of the British Museum (Natural History) and Mr. F. Ballard of the Royal Botanic Gardens, Kew, for much help; to the Director of Agriculture, Peradeniya, Dr. Joachim, and to the Assistant Director, Mr. Joseph, for transport facilities; to Mr. Jayaweera, Peradeniya, and his assistants for much help; to Mr. T. B. Worthington of Kandy for his very generous hospitality; and to Mr. B. Clarke, Leeds, for photographic help.

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STUDIES ON COMPETITION IN PLANTS AND ANIMALS. IX. EXPERIMENTAL STUDIES ON MIGRATION IN *DROSOPHILIA MELANOGASTER*[1]

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A number of experiments have been conducted on the competition between different races of a Drosophila species or between different species of the same genus (Reed and Reed, 1950; Ludwin, 1951; Moore, 1952; Merrell, 1953a, b; Tebb and Thoday, 1954; Birch, 1955; For further literatures published before 1950 refer to Dobzhansky, 1951). However, all of them dealt with the competition occurring between different strains kept within a limited space of the population cages or population-bottles. If two genotypes differ from each other with respect to either propagating capacity or competitive ability, they will show differential survival after a number of generations if they are kept mixed in the cage or bottle. But what should we expect to occur in a mixed population of flies if it is kept in an open space as found in wild populations? The weakly competing flies might seek for a new niche, establishing a new population there, instead of being destroyed, even if they could not compete against the strongly competing flies in the old niche. How about the effect of competition upon two genotypes mixed in a population under such circumstances?

There is a problem to be investigated, however, before entering the above problem. That is: What is migration in Drosophila flies? Our knowledge concerning migration in Drosophila flies seems to be very scanty up to present. Thus, we have planned experiments on migration of the flies. The present paper describes the results of our experiments conducted since the beginning of 1956.

The investigations aim at solving following two questions:

(1) Is the occurrence of migration in Drosophila flies from one place to another dependent upon density of population or upon random movement of individual flies?

(2) Is there any racial difference with regard to migrating activity?

MATERIAL AND METHOD

At the end of the year 1955, a number of glass tubes each having a bottom and three radial branches on its periphery were constructed in our laboratory. They are called by us the "population-tubes," size and structure of which and a set of four tubes combined for the study of migration are shown in figure 1.

A number of population-tubes can be connected with each other by short small vinyl-resin tubes at the radial branches. When they are connected with each other, they resemble the "stepping-stone" model as discussed by Kimura (1953).

The stock used in the first part of this experiment was the Samarkand strain, a well known laboratory stock inbred for more than 300 generations. The strains used in the second part of the experiment were six wild strains collected from the corresponding number of localities in Japan in the fall of 1956. The names of strains and the localities where they were collected are presented in table 1.

Katunuma-cho, Yamanashi-ken, is a town surrounded by spreading vineyards. The KN strain was collected at the heap

[1] Contributions from the National Institute of Genetics, Japan, No. 209.

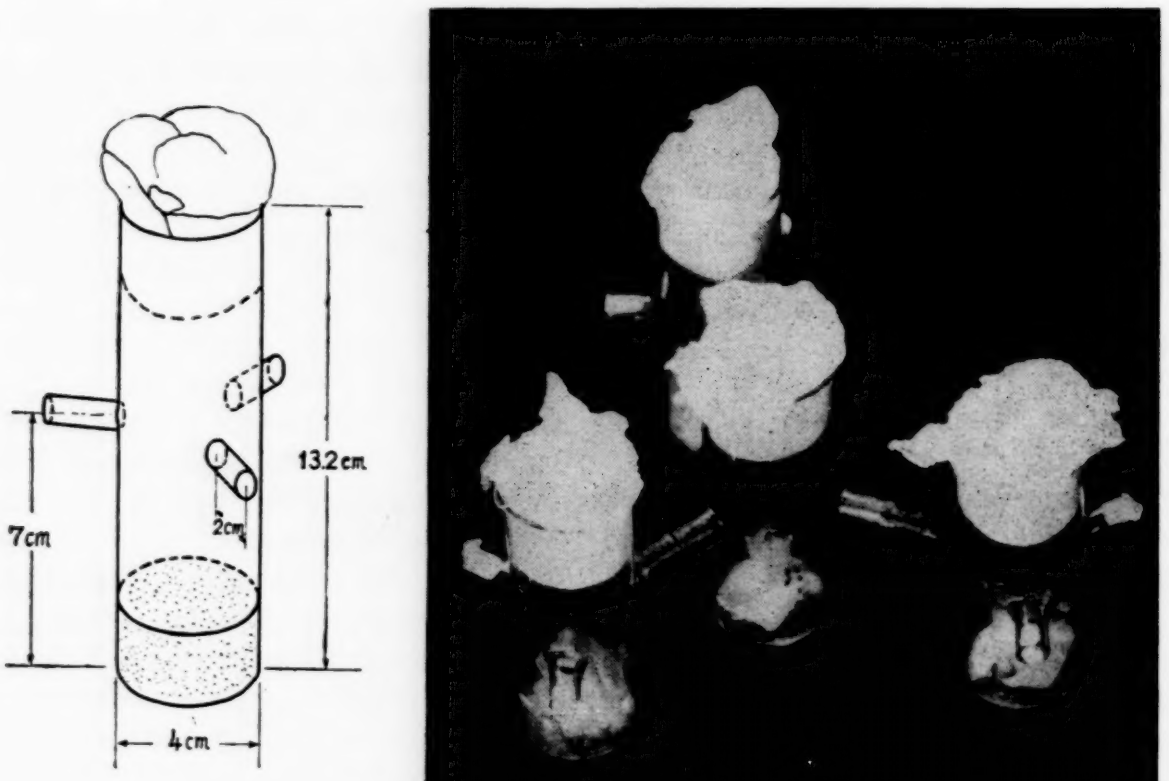

FIG. 1. (A) The population-tube, its size and structure. (B) A set of four population-tubes combined for the study of migration.

of lees in a brewery of wine, where numberless flies were swarming. The other five strains were collected on five islets distributed not far from each other in the Inland-Sea of Seto.

One experimental plot consists of four population-tubes, each containing about 1.5 cm of cornmeal-molasses-agar medium with yeast on its surface. On the first day of experiment, a definite number of flies was introduced into one of the four tubes. After keeping flies in the tube for one day, the three vacant tubes were connected to it by the vinyl-resin tubes. The combined four population-tubes were then placed in a dark room regulated at 25° C.

After definite periods of time, the number of flies migrated into the three additional tubes was counted. In the case of relatively small numbers of migrated flies, the counting was made without any difficulty, but, as the number increased, the tubes were disconnected one by one to avoid miscounting.

TABLE 1. *Description of six wild strains collected in the fall of 1956*

Names	Localities	Prefectures
KN	Katunuma-cho	Yamanashi-Ken
TB	Tateba-sima*	Okayama-Ken
KS	Kama-sima*	Okayama-Ken
IG	Iguro-sima*	Kagawa-Ken
TS	Te-sima*	Kagawa-Ken
IS	Isima*	Kagawa-Ken

* Sima means an islet.

EXPERIMENTAL RESULTS

Experiment with the Samarkand Strain

The experiment started with introduction of various number, ranging from 30 to 300, of flies of the Samarkand strain into original tubes. Each of the original tubes were connected to three vacant tubes on the next day, and the number of migrated flies in the additional three tubes was counted on the fourth day. Mean number of migrated flies in percentage

TABLE 2. *Number in per cent of migrated flies after two days of connection of additional tubes. The Samarkand strain*

	Number of flies introduced in the original tube					
	0–49	50–99	100–149	150–199	200–249	250–300
Number of observations	4	4	6	7	6	5
Number of migrated flies (%)	5.21	2.31	1.89	23.47	26.49	24.93

of the total number introduced in the original tube is presented in table 2 and, in more detail, in figure 2.

The result of the experiment presented in table 2 or in figure 2 suggests that migration of flies of the Samarkand strain is likely to take place as a threshold reaction to the density of population: the critical density appeared to be 150.

The next experiment using the Samarkand strain was to find the relation between number of migrated flies and the periods of time during which the migration was allowed to take place. Counting was made at 6, 24, 48, 72, 96, 120, and 144 hours after the connection of additional tubes. Results of the experiment can be summarized in table 3 and are presented graphically in figure 3.

From table 3 as well as in figure 3, we find that, after the 24-hour period, percentage of migrated flies increases approximately linearly in proportion to the length of time during which the migration is allowed to take place. Statistical test for deviations from linear regression of four groups of data proved that they were not significant statistically. The

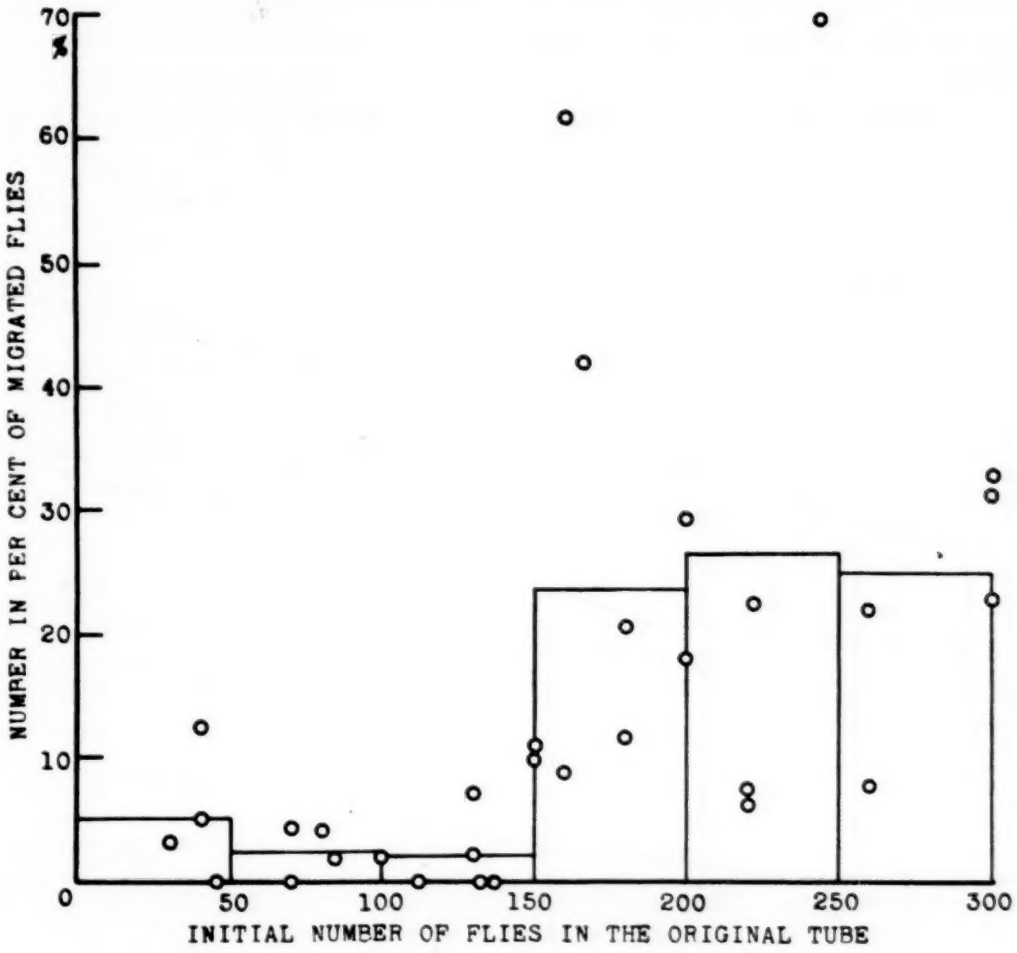

FIG. 2. Relation between number of flies introduced into the original tubes and number in per cent of migrated flies during the period of 48 hours. The Samarkand strain.

TABLE 3. *Number in per cent of migrated flies during seven periods of time from 6 to 144 hours*

No. of flies introduced into original tubes	No. of experiments	No. in % of migrated flies after						
		6	24	48	72	96	120	144 hrs
100–149	5	1.84	0.59	2.25	3.32	5.52	6.51	7.21
150–199	4	14.66	11.02	13.31	14.51	20.95	22.47	25.01
200–249	4	14.92	14.47	15.41	18.47	23.50	24.59	24.00
250–300	5	19.59	21.35	24.39	27.55	29.90	32.46	32.91

difference among regression coefficients of four lines was also found not to be statistically significant (table 4).

The average increase of migrated flies was 2.2481 per cent per day of the population. This increase in the number of migrated flies appears to be caused by the individual activity of flies to move at random without regard to the density of population. On the contrary, a good deal of migration occurring in the first six-hour period when the initial size of population exceeded 150 must have been caused by the pressure of population density. Thus, two kinds of migration were found to occur: one, the so-called "mass migration," which occurs as the result of pressure of population density and the other, the so-called "random migration" as the result of random movement of individual flies.

Experiment with Wild Strains from Six Localities in Japan

Six wild strains as described in table 1 were used in the present part of experiment. After keeping the collected flies by random-mating for two or three generations in half-pint milk bottles in the laboratory, the six strains were tested for their migrating activity. The experiment was at first conducted at three levels of population density; that is, 80, 120, and 160 flies in the original tubes. The experiment was replicated four times.

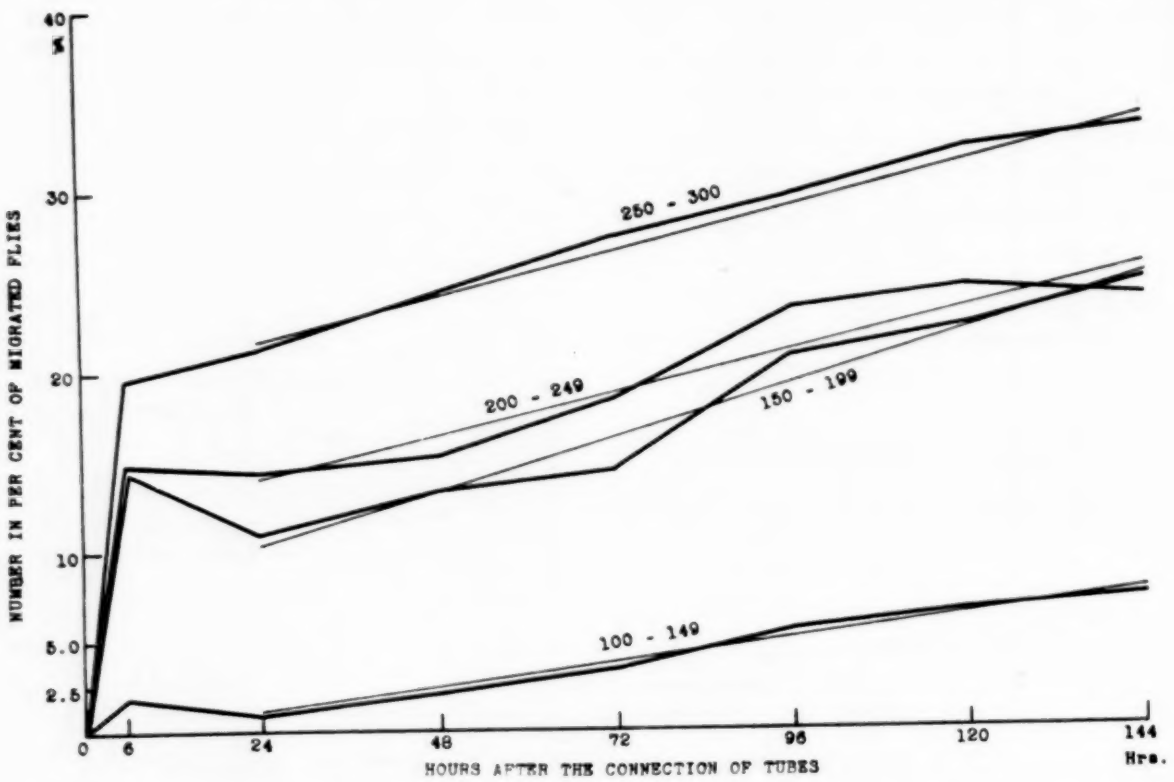

FIG. 3. Migration of flies of the Samarkand strain of *D. melanogaster* at 6, 24, 48, 72, 96, 120 and 144 hour-periods after the connection of additional tubes. The fine straight lines running from 24- to 144 hour-periods are regression lines fitted to data.

TABLE 4. *Test of significance of differences among four regression coefficients*

Source of variation	d.f.	Mean square
Differences among regressions	3	16.17
Error	16	30.64

As most of the percentage data obtained lay between 30 and 70 per cent, analysis of variance was conducted without any transformation of percentage values. The result of analysis of variance is presented in table 5.

It is seen from table 5 that variation due to strains and that due to population density were both statistically significant. The average percentages of migration based on four replicated experiments are presented in table 6 for six wild strains.

Tables 5 and 6 show that there is a difference regarding migrating activity among the six wild strains and that, remembering table 2, wild strains differ from the Samarkand strain in that the former are very active in migration in comparison with the latter. In addition, wild strains contrast with the Samarkand strain in that the latter never approached the amount of mass migration shown in the former even at so low level of population density as 80.

The following question then arises: Doesn't a mass migration such as found in the Samarkand strain occur in those wild strains at any level of population density?

TABLE 5. *Analysis of variance of number in per cent of migrated flies at 48-hour period at three levels of population density of six wild strains of* Drosophila melanogaster

Source of variation	d.f.	Mean square
Population density	2	308.98*
Local strain	5	489.31**
Density × strain	10	44.46
Replication	3	113.17
Error	51	67.48

*, ** Significant at the 5% and the 1% levels, respectively.

TABLE 6. *Percentages of migrated flies in six wild strains of* Drosophila melanogaster *at three levels of population density*

	Percentages of migrated flies at the population density of			
	80	120	160	Mean
IS	55.63	60.73	55.74	57.34
KN	55.00	55.83	64.84	58.56
TS	50.06	59.25	57.66	55.64
KS	48.75	55.21	58.75	54.24
IG	44.32	53.31	54.69	50.78
TB	39.50	40.85	42.81	41.05

In order to get an answer to this question, further experiments with lower levels of population density than 80 were conducted. The experiments were replicated four times for each level. Table 7 presents the analysis of variance of data obtained. In this case, the obtained data expressed in percentage were transformed into the form $\varphi = \sin^{-1}\sqrt{p}$ before analysis. It is interesting to find that variation due to interaction between density and strain was highly significant.

The average percentages of migrated flies for six wild strains at four levels of population density are presented in table 8 together with those of the Samarkand strain. The Samarkand strain was tested for its migrating activity at comparable levels of population density. Replication in this case was also made four times.

The whole data presented in tables 6 and 8 and also the comparable data concerning the Samarkand strain are illustrated graphically in figure 4.

It is apparent in figure 4 that there is

TABLE 7. *Analysis of variance of percentages of migrated flies of 6 wild strains of* D. melanogaster *at four different levels of population density: 10, 20, 40 and 60*

Source of variation	d.f.	Mean square
Population density	3	1439.76**
Local strain	5	320.95
Density × strain	15	124.52**
Replication	3	51.87
Error	69	35.02

** Significant at the 1% level.

TABLE 8. *Average percentages of migration at four levels of population density in 6 wild strains and the Samarkand strain*

	Percentage of migration at the population density of			
	10	20	40	60
IS	20.00	20.00	26.88	42.97
KN	20.00	20.00	55.00	57.08
TS	17.50	15.00	23.75	42.92
KS	17.50	10.00	13.75	36.69
IG	10.00	15.00	40.00	39.90
TB	25.00	13.75	19.38	22.08
Samarkand	5.00	6.20	3.75	4.50

TABLE 9. *Number in per cent of migrated flies during four days*

Initial size of population in the original tube was 80 flies. Mean values of four replications.

	Number in per cent of migrated flies at			
	1-day period	2-day period	3-day period	4-day period
KN	38.44	54.38	75.94	88.44
KS	41.25	49.06	64.38	85.00
IS	29.69	50.63	67.19	83.13
IG	24.06	41.88	71.56	89.06
TS	33.06	43.44	55.94	75.31
TB	19.06	33.75	54.38	80.63

a striking difference among strains with regard to the level of population density at which mass migration occurs. For instance, mass migration occurs in KN (Katunuma) strain at the density of 40, while in TB(Tateba) 80. Mass migration occurs in the IG(Iguro) strain at the density of 40, while in IS(Isima), TS(Tesima) or KS (Kamasima) strains between 60 to 80. One glance of figure 4 will enable us to divide the six wild strains into three or four groups according to migrating activity.

There arises still another question: Is there any inter-strain difference with regard to intensity of random migration?

To get an answer to this question, an experiment was conducted, in which eighty flies of each strain were introduced into the original tube and the number of migrated flies was counted every day during the period of four days. The experiment was replicated four times. The results, averaged on the basis of four replications, are presented in table 9.

Statistical test of linearity of six groups

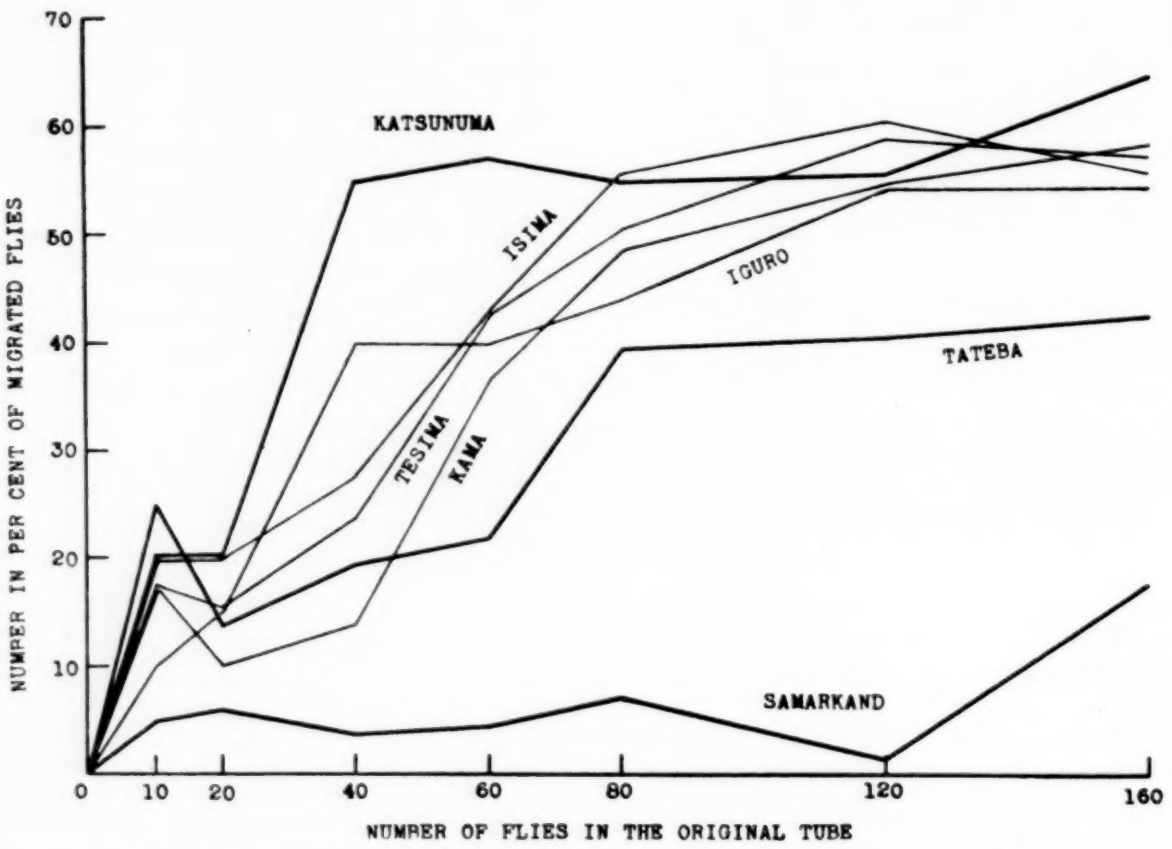

FIG. 4. Results of migration experiment with 6 wild strains and the Samarkand strain of *D. melanogaster*.

of data proved that the increase in percentages of migration was linearly proportional to the number of days during which flies were allowed to migrate. Statistical test of difference among six regression coefficients was also conducted, result of which is presented in table 10. Table 10 shows that differences among regression coefficients of six strains is statistically highly significant. The 95% fiducial intervals for the six regression coefficients are as follows:

IG strain $18.9167 < 22.4688 < 26.0209$
TB strain $17.8198 < 20.5313 < 23.2428$
IS strain $15.5180 < 17.6875 < 19.8570$
KN strain $15.6325 < 17.1562 < 18.6801$
KS strain $11.5765 < 14.6563 < 17.7361$
TS strain $12.4403 < 13.9250 < 15.4097$

TABLE 10. *Test of significance of differences among 6 regression coefficients*

Source of variation	d.f.	Mean square
Differences among regressions	5	218.24**
Error	84	33.78

** Significant at the 1% level.

The regression coefficients described above stand undoubtedly for the activities of migration due to random movement of individual flies. In respect of these activities, the six strains may be arranged in the order of high to low as follows:

(High) (Medium) (Low)
$IG \geqq TB > IS \geqq KN > KS \geqq TS$

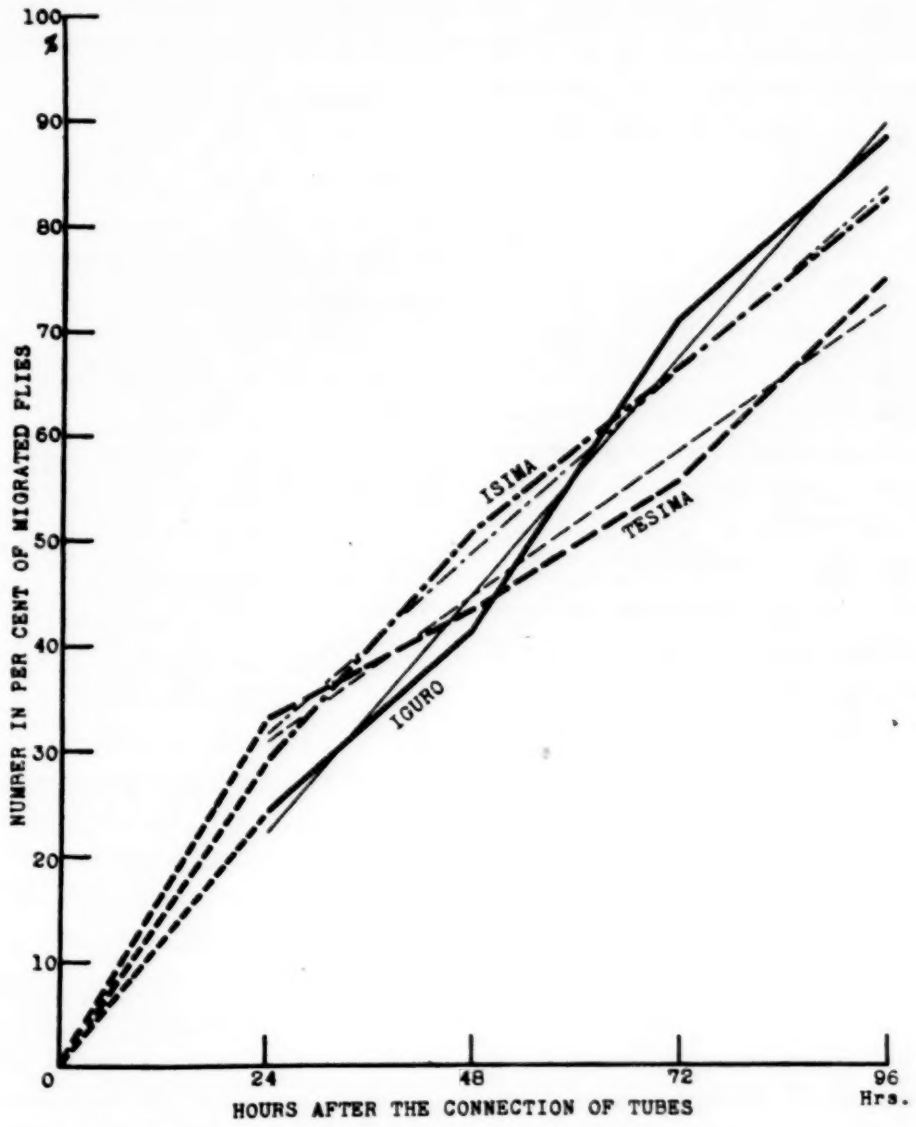

FIG. 5. Graph illustrating activities of migration of three wild strains of *D. melanogaster*. Thick and thin lines represent experimental and regression lines, respectively.

Data of the three representative strains one from each group and the corresponding regression lines are shown graphically in figure 5.

Discussion

As described at the beginning of this paper, the competition experiments with Drosophila flies have been conducted mainly in a closed cage or bottle, where flies cannot release themselves from the competitive state to find a new niche. In wild conditions, however, the story must be quite different. The writers have been interested in the study of competition in plants and also in animals. They think that competition particularly in animals should be investigated not only in closed space, but also in a space of more or less independent regions. Thus the so-called population-tubes were constructed and, before entering the problem of competition, migration has been investigated using Drosophila melanogaster.

The former part of the experiment dealt with the migration in the Samarkand strain of Drosophila melanogaster, which are highly inbred and tamed in laboratories. In this strain, it was found that two kinds of migration occurred. One was, so to say, the mass migration, which occurred when the size of the population in the original tube exceeded 150. The other was, so to say, the random migration, which occurred at any time in any population without regard to the density of population. The intensity of random migration in the Samarkand strain was 2.25% per day.

The latter part of the experiment dealt with the migration in six wild strains collected from the same number of localities in Japan. It was found in this part of the experiment that the wild strains were strikingly active in migration in comparison with the Samarkand strain. They were not only more active than the Samarkand strain in random migration, but also in mass migration. For instance, frequencies of random migration per day of the six wild strains were more than 20% in two of them, about 17% in other two, and about 14% in the remaining two strains. Regarding mass migration, it occurred in some strains at so low density as 40 flies in the population while in others at the density of 60 to 80. The whole experimental results can be summarized regarding two kinds of migrating activity as follows:

Strain		Lowest level of population density causing mass migration (number of flies)	Intensity of random migration per day (%)
Wild	IG	40	22.47
	TB	80	20.53
	IS	60–80	17.69
	KN	40	17.16
	KS	60–80	14.66
	TS	60–80	13.93
Samarkand		150	2.25

It will be quite natural and interesting to assume that differential response of different strains regarding level of population density causing mass migration would be controlled by genetic nature of the population. Also of interest will be to assume that activity of random migration would be genetically controlled.

The five wild strains, IG, TB, IS, KS and TS were collected from five islets distributed in the Inland-Sea of Seto. They lie not far from each other though completely separated by water. It is of interest to find that wild populations of *Drosophila melanogaster* collected from those islets differed from each other with respect to both activities of migration.

In the present experiment, it has been found that the Samarkand strain was unusually weak in activity of either random or mass migration. The strain has been inbred for more than three hundred generations and at the same time must have been acclimated to the condition of small containers for the same number of generations. Is the weak activity of the strain the result of inbreeding or that of acclimation? The problem is left unsolved.

Conclusions

Results obtained in this experiment lead us to draw the following conclusions:

(1) There are two kinds of migration occurring in a population of *Drosophila melanogaster:* One is the so-called "random migration" which takes place as a result of random movement of individual flies, and the other is the so-called "mass migration" caused by the pressure of population density.

(2) The intensity of random migration differs from strain to strain. In an highly inbred and domesticated strain, the intensity was so low as 2.25% of total population per day, while in wild strains, it was as high as 14 to 20%, though inter-strain differences were still pronounced among them.

(3) The lowest density of population causing mass migration also differs from strain to strain. In the inbred laboratory strain, it occurred when the number of flies introduced into the original tube exceeded 150, while in wild strains, the critical density was 40 in some and 60 or 80 in others.

(4) Such inter-strain differences in both activities of migration seem to be of genetic nature.

(5) Five wild strains collected from the same number of islets distributed in a relatively small area of Inland-Sea of Seto, were compared regarding both activities of migration. Inter-strain differences were found in both activities of migration, probably as the result of isolation and/or selection.

Summary

Migration experiment was conducted with laboratory and wild strains of *Drosophila melanogaster*. Equipment constructed for this experiment is called "population-tubes" each having three protruding branches on its periphery. Experimental results obtained lead us to divide migration in the fly populations into two kinds: One, the "random migration" which occurs as the result of random movement of individual flies, and the other, the "mass migration" as the result of pressure of population density. Inter-strain differences in both activities were very pronounced, and it is assumed that these activities would be under genetical control.

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STUDIES ON BLOOD GROUPS IN THE AMERICAN BISON (BUFFALO)[1]

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The antigenic characteristics of red cells provide unusual advantages for the analysis of genetic similarities and differences among related species. This opportunity has been most extensively exploited in the analysis of relationships among various species of pigeons and doves (cf. Irvin, 1953) and in ducks (McGibbon, 1944). Rather numerous studies have been made also of the occurrence of antigenic factors related to those found in human blood, as they occur in other animals (cf. Wiener, 1943). The most common experience in such studies has been to find that antigenic materials similar to, but often not identical with, the antigens segregating or fixed in a given species are either segregating or fixed in a related species. There has been little basis for evaluating the degree of such relationships in terms of the evolutionary affinities of the populations concerned.

Some years ago, we undertook to capitalize on the availability of a large battery of antibody reagents distinguishing individual differences in cattle, for the investigation of this kind of problem. Several levels of taxonomic diversity were subjected to study, beginning with differences within and between breeds of dairy cattle, as representative of differences at the racial level (Owen *et al.*, 1947), and progressing through a series of Brahma cattle (unpublished; the differences here proved representative of rather extreme breed differences), and on to a species comparison. The last-named of these categories is the subject of the present paper.

At the time of the initiation of these studies on bison, we had at our disposal a battery of blood typing antibodies used in the differentiation of nine genetically independent blood group systems in cattle. These antibody reagents were used in typing the bloods of sixty-nine bison—some from the Wichita Mountains Wild Life Refuge at Cache, Oklahoma, and some from the National Bison Range, Moiese, Montana. This study was later followed by a survey of cattalo (hybrids and back cross hybrids from the crossing of domestic cattle and bison). Finally, attempts were made to demonstrate a species difference between bison and domestic cattle by means of a classical method, namely, antibody-absorption experiments employing heteroimmune (rabbit) antiserum against the bloods of individual bison and cattle, and heteroimmune cattle serum against the blood of individual bison. This report is concerned with a description of the results of the various studies mentioned.

Materials and Methods

The blood-typing tests on bison red cells were performed in the manner described by Stormont *et al.* (1951) and Stormont (1947, 1952), in their studies of nine blood-group systems B, C, F-V,

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Z, S-U, A-H, H′, J and Z′ of domestic cattle. The bovine blood-typing tests are "hemolytic" tests in which pooled, fresh-frozen normal rabbit serum is used as complement. The sera of rabbits having more than negligible amounts of natural antibodies reactive with cattle or bison red cells were not used.

The bison cells were tested with the bovine blood-typing reagents or antibodies B, G, I, K, O_1, O_2, O_3, P, Q, T_1, T_2, Y_1, Y_2, D′, E'_1, E'_2, E'_3, I′, J′ and K′ known to differentiate the products (phenogroups) of at least 160 alleles at the B locus, the reagents C_1, C_2, R, W, X_1, X_2, and L′ known to differentiate the phenogroups of more than 25 alleles in the C set, the reagents F and V which differentiate the paired alternatives F and V, the reagents S, U_1 and U_2 which differentiate the phenogroups of five alleles in the S-U set, the reagents A and H which differentiate the phenogroups of four alleles in the A-H set, and the reagents J, Z, H′ and Z′ which differentiate a pair of alternatives (J as contrasted with no-J, etc.) in each of the systems, J, Z, H′ and Z′, respectively, in cattle. The cattalo cells were tested with these same reagents and, in addition, with A′ of the B system (which had been temporarily exhausted at the time of the bison tests) and with a new reagent, designated L, which differentiates a pair of alternatives (L as contrasted with no-L) in a tenth system of bovine blood groups (Stormont, unpublished).

Heteroimmune rabbit antisera were prepared as described in the papers already cited. Cattle antisera against bison blood were prepared by injecting (intravenously) 25 ml of whole, citrated blood for three injections at weekly intervals. The resulting antisera were collected eight days after the last injection.

Results

Tests of the sixty-nine bison bloods were essentially negative for the entire battery of twenty B-system reagents. All bloods were completely negative with reagents H′ and Z′, respectively. The same was true with reagents R of the C system, U_1 and U_2 of the S-U system and H of the A-H system. The phrase "essentially negative" with the entire B system is to be taken with some reservation, because actually certain of these reagents, notably E'_3 and J′, produced slight degrees of hemolysis with certain of the bison bloods. When tested by absorption, these slightly reactive bison bloods proved capable of absorbing part of the antibodies for cattle cells, while absorptions with positive (and not with negative) cattle cells removed the reactivity for the positive bison cells. Other slight reactions occurred occasionally with the B-system reagents O_1, O_2, O_3, T_2 and Y_1. These are referred to the category "atypical" or negligible reactions because absorption studies in these instances indicated that the bison reactions were not due to the specific antibodies for which the reagents are used to distinguish individual cattle.

On the other hand, all bison bloods were positive with the reagents X_1, X_2 and L′ of the C system and reagent V of the F-V system. The reactions with the L′ reagent were extremely weak and low-grade. Furthermore, there was no convincing evidence following absorption of the L′ reagent with bison bloods that the reactions with L′ were of the nature of true cross reactions. On the other hand, the cross reactions of all 69 bison bloods with X_1 and X_2 reagents were as strong as, or stronger than, the best reactions obtained with cattle blood, and all bison bloods completely absorbed these reagents.

Although, as mentioned, all bison bloods were positive with reagent V, it was apparent that the hemolysis with this reagent, even though often going to completion, was proceeding at a much slower rate than that observed in testing known V-positive cattle bloods. Absorptions of the V reagent with bison bloods clearly demonstrated that these reactions were of the nature of true cross reactions, since the titer of V antibodies for known B-positive cattle bloods was considerably

reduced. By careful absorption, it was possible to exhaust the cross reactive fraction and leave a residual fraction (designated V_1) that reacted with the bloods of V-positive cattle but not with bison blood. These tests therefore distinguished two sub-types of blood factor V, the one designated V_1, peculiar to individual cattle, and the other designated V_2, present in all bison tested.

Each of the remaining reagents, namely A, C_1, C_2, J, S, W and Z, reacted with some but not all of the bison bloods. With few exceptions, the time-course of the reactions and degrees of hemolysis obtained with these seven reagents were essentially the same as those seen in testing cattle bloods. Also, Z "dosage" reagents which differentiate homozygotes (*ZZ*) from heterozygotes (*Zz*) in the Z system of cattle (Stormont, 1952) gave parallel reactions with bison bloods. Furthermore, when these individual reagents were absorbed with reactive bison bloods, the antibodies for cattle bloods were exhausted. Consequently, the conclusion seemed to be justified that individual American bison contain certain erythrocytic antigens which are closely similar if not identical in at least a portion of their structure to some of those antigens that make for individual differences in cattle. These are the bison antigens which cross react with antibodies in the bovine blood-typing reagents A, C_1, C_2, J, S, W, X_1, X_2 and Z. The same sort of conclusion is of course justified for blood factor V but here it is certain that the V factor of bison and V of domestic cattle are not identical. In addition we noted that all bison samples were V-positive in contradistinction to domestic cattle where only a fraction of the various breeds so far sampled has been V-positive.

The special position of blood factor J, the only one of the bovine blood factors dependent on a normal isoantibody reagent, should be noted here. The erythrocytes of some bison reacted to this reagent, while others did not. When present, the reactivity appeared to differ to some extent among individual bison; the J reagent from cow 17Z could be fractionated by careful absorption so that the partially-absorbed fluids distinguished, as in cattle, different degrees of reactivity. The situation appears comparable to that prevailing for the normal human isoantibody β (Owen, 1954) and is relevant to other studies of anti-J in cattle and other animals (Stormont, 1949; Sorensen *et al.*, 1954).

A comparison of the frequencies of blood factors A, C_1, C_2, J, S, W and Z in the two bison populations, one represented by samples from animals of the Montana refuge and the other by animals of the Oklahoma refuge, is given in table 1. The quantitative reliability of these frequencies as representative of the populations from which they came is questionable, because there is no information on the relationship of individuals within either sample, and the samples are small. Taken as they stand, significant differences between the two samples are indicated for the frequencies A, J, and W, but not for C_1, C_2 and S. For Z the complete genotypic

TABLE 1. *Summary of frequencies of bovine-like blood factors in samples of the two bison populations*

("Bi" = 44 animals from the Oklahoma refuge; "BR" = 25 animals from the Montana refuge.) The number given first in each category represents the number of individuals giving positive reactions for the factor; the decimal number in parentheses is the calculated frequency of the positive alleles. The symbols Z^S and Z^W refer, respectively, to strong reactions and weak reactions with Z dosage reagents.

	A	C_1	C_2	J	S	W	Z^S	Z^W
Bi	17(.21)	5(.06)	7(.08)	28(.40)	15(.19)	17(.21)	8(.33)	13
BR	2(.04)	0(.00)	0(.00)	4(.08)	11(.25)	2(.04)	2(.38)	15

ratio in each sample is easily determined, because the class labelled Z^w is heterozygous for Z, while that labelled Z^s is homozygous. Here, the gene frequencies in the two samples are remarkably similar ($p_z = .33$ for the Oklahoma refuge, .38 for the Montana refuge).

Subsequently, samples were obtained from fifty-one cattalo in the Buffalo Enclosure, Wainwright, Alberta. Ten of these were female F_1 hybrids out of bison cows and sired by domestic bulls (Aberdeen-Angus, Hereford and Shorthorn). The forty-one remaining hybrids were from F_1 females and backcross females mated to domestic bulls or near-domestic bulls. We are indebted to Mr. P. E. Sylvestre of the Central Experimental Farm at Ottawa for making arrangements for the collection of the samples and assisting in the corralling and bleeding. Unfortunately, since the animals were range-bred, there was no precise pedigree information on the actual parents of the back-cross hybrids. Furthermore, the parents of the F_1 females were deceased. Nevertheless, some information of additional interest was obtained in blood-typing the F_1 hybrids. We shall confine our discussion to the results obtained on the F_1 hybrids and specifically to the blood-group systems B, C, F-V and L.

Three of the F_1 hybrids had the color-markings (white face and brindle body) expected of a cross between bison and Herefords (see Deakin *et al.*, 1942). Consistent with this was the fact that two of these white-faced hybrids possessed the B system phenogroup $Y_1D'I'$ and the other possessed A′ (presently designated O_xA' in the California Laboratory), each of which occurs frequently in animals of the Hereford breed. Likewise, six of the F_1 females had the color markings (solid dark brown often with a shadow brindle pattern) expected of a cross between pure bison and Aberdeen-Angus. Four of these had phenogroup $Y_2E'_1$ (presently designated $Y_2E'_14$ in the California Laboratory), one had phenogroup $GY_2E'_1$ and one had phenogroup E_3' (either O_xE_3' or $O_xE_3'8$ in present terms) all of which are recognized as relatively frequent in the Angus breed but not so in Herefords and Shorthorns. The remaining F_1 female had the brindle pattern expected from a mating of bison and Shorthorn. Her cells were reactive with the G and A′ reagents of the B system but these results could not be accounted for on the basis of any one of the known B phenogroups in Shorthorn cattle. The possibility that this animal may have been a first backcross female rather than an F_1 hybrid could not be excluded.

All ten of the F_1 hybrids had blood factor X_1 as would be expected if the bison parents were uniform for C phenogroups reactive with X_1 and X_2 reagents, a result consistent with our observation that all of sixty-nine bison possessed X_1. In addition to X_1 all of the F_1 females possessed blood factor C (seven C_1 and three C_2). Three had blood factor W and one had both R and W, in addition, of course, to C and X_1. In the absence of blood-typing information on their parents and/or offspring, it was not possible to determine the precise C phenogroups in these hybrids.

The results in the F-V system were of particular interest. Nine of the F_1 females possessed both of the blood factors F and V_2, and it can be assumed that F was transmitted solely by the domestic parents and V_2 solely by the bison parents. It would be conventional therefore to write their F-V phenogroup formulas as F/V_2. In view of previous experience (Stormont, 1952) in testing domestic cattle of formula F/V, it might be expected that the cells of the F/V_2 hybrids would, like F/V domestic bloods, exhibit markedly reduced degrees of hemolysis in tests with so-called F "dosage" reagents. This, however, was not the case. The cells of the F/V_2 cattalo reacted as well with F dosage reagents as do those of domestic cattle homozygous for phenogroup F (formula F/F). This observation provides an indication of an F-like property of V_2, which is supported by

more recent and critical data to be reported elsewhere (Stormont, unpublished).

As already mentioned, attempts were made to demonstrate clear-cut species differences between bison and domestic cattle by means of the classical antibody-absorption experiments employing heteroimmune antisera (Ehrlich and Morgenroth, 1901). For example, Ehrlich and Morgenroth had shown that rabbit antisera to ox blood acts on goat blood as well as cattle and, conversely, rabbit antisera to goat blood acts on cattle blood. By cross-absorbing, they were able to show that each of the two kinds of antisera contained two major fractions of immune body. The rabbit anti-cattle sera contained one fraction active on both goat and cattle blood which could be exhausted by absorbing with goat blood. The residual fraction acted only on cattle blood and its solvent power (or titer) was essentially that of the unabsorbed serum. Likewise, absorption of the cross reactive fraction in rabbit anti-goat serum left a residual fraction for goat cells which had essentially the same solvent power as the unabsorbed serum. Precisely the same results were obtained by Irwin and McGibbon, in papers already cited, in their studies of relationships among various species of birds. Our tests, following absorption of eight rabbit anti-cattle and ten rabbit anti-bison sera, however, failed to yield unequivocal results indicative of a clear-cut species difference. On the contrary, absorption of these antisera with the cells of selected individuals of the heterologous species and with the pooled cells of several selected animals of the heterologous species often succeeded in absorbing the antibodies for the homologous species. A few promising anti-bison fractions were indicated in some of these absorptions. We would hesitate to state, however, that any of these antisera contained antibodies reactive with all individuals of the homologous species to the exclusion of all individuals of the heterologous species. Subsequently, attempts were made to demonstrate species antigens in bison by immunizing cattle with the blood of individual bison and cattalo. Again, there was no indication of a definitive, truly bison specific fraction in these cattle anti-bison sera. These results demonstrate no major species antigens specific to bison in contrast to domestic cattle. An abstract reporting later studies suggesting a different conclusion has been published by Miller and Stone (1955).

As expected, reagents specific for such blood factors as A, S and V found in both species appeared after the absorptions of the rabbit and cattle heteroimmune sera. Of particular interest was the observation that anti-bison V reagents reacted equally with V of domestic cattle and V of bison. Furthermore, the anti-bison V reagents (anti-V_2) were readily absorbed by V-positive (type V_1) cattle bloods. These results, in line with those obtained by Stormont (1950) in studies of the subtypes of such bovine blood factors as C, T and U, fortify our interpretation that blood factor V_2 of bison is truly a serological sub-type of V (or V_1) of domestic cattle.

Specific V_1 reagents were prepared by absorbing standard anti-cattle V reagents with either bison blood (V_2/V_2) or cattalo blood of formula F/V_2. These V_1 reagents were run in parallel with our standard V reagents in routine blood-typing tests on the bloods of several hundred domestic cattle but none was ever encountered whose cells reacted only with standard V. Consequently, if V_2 exists in domestic cattle, it is very rare in the breeds studied by us.

Finally, it should be mentioned that the bison bloods used in the second group of immunizations were tested against our battery of bovine reagents which contained a comparatively new reagent named L. This reagent differentiates a pair of phenogroups L and no-L in a tenth system of bovine blood groups. All six bison bloods were reactive with and capable of exhausting the L antibodies. However, the fact that some of the F_1 hybrids were

L-negative would indicate that this blood factor is not fixed in bison.

Discussion

In his critical study "The North American Buffalo," Roe (1951, p. 3) listed seven taxonomic names (*Bison americanus, Bos americanus, Bos* (*Bison*) *bison,* etc.) for the so-called "Prairie Buffalo" of North America, and three for the so-called "Wood Buffalo" of North America. Quoting Hornaday, Roe went on to state, "In the United States, this animal has generally borne the name buffalo, though discriminating writers persist that the name is erroneous, and that it should be called the American bison. The latter is undoubtedly its correct English cognomen, but probably among people generally the name *buffalo* will never be supplanted." Aside from the problem of what name to use in referring to this beast is the problem of taxonomic classification. Whether indeed the American buffalo or bison should be classified in a genus separate from the genus Bos which includes the various breeds or sub-populations of domestic and wild cattle and whether indeed the Prairie and Wood buffalo, or for that matter the Musk Ox (see Roe, 1951), deserve taxonomic recognition as distinctly different species are questions which will undoubtedly be with us for some time.

There are no formal criteria whereby blood-typing antibodies developed for the purpose of differentiating individuals within a species (as cattle) may be used in differentiating species of the same or a different genus. It has been established that most of the bovine blood factors differentiated by the battery of reagents used in the present study have significantly different frequencies in the different breeds of domestic cattle of European origin (Owen *et al.,* 1947; Stormont, 1952). Often of greater magnitude and significance are the between-breed differences in the frequencies of alleles at each of the various loci (Stormont *et al.,* 1951). We might expect that between-species differences in the frequencies of individual blood factors and alleles might be more extreme than those seen between races or breeds within a species.

While there are many aspects of the reactions of bison bloods with bovine blood-typing antibodies reminiscent of the order of differences seen between breeds of domestic cattle, there are nevertheless certain striking contrasts. Those differences include: (1) the virtually complete non-reactivity of bison bloods in tests with 19 different reagents reactive in the B system of cattle, an observation which has had no parallel in equivalent samples of various domestic breeds of cattle of either European or Asiatic origin, (2) the complete non-reactivity of bison bloods with H′ reagent, in contrast to the regular appearance of this factor with high frequency in equivalent samples of various breeds of cattle, (3) the observation that the products of all *C* alleles in bison cross react strongly with the C system reagents X_1 and X_2, while in cattle the products of numerous *C* alleles do not react with these reagents, and (4) the indication of an allele F^{v_2}, controlling a phenogroup V_2, which on the basis of the present study would seem to be fixed in bison but has so far not been recognized in domestic cattle. Other differences, such as the failure of all sixty-nine bison samples to react with the reagents R, U_1, U_2, H and Z′, cannot be regarded as meaningful, since each of these blood factors is of rather low frequency in most of the breeds of cattle so far studied. Of the differences enumerated, that concerning blood factor V_2 appears to be the most definitive, especially in the light of our failure to demonstrate a significant difference between the two species by means of the classical method of cross-absorbing heteroimmune rabbit antisera.

It remains here to raise the interesting question of the extent to which our present samples of bison may be representative of the great herds of buffalo that once roamed the American prairie. The histories of the populations we have ex-

amined are given by Garretson (1938) and Ruth (1937). We have also had the benefit of personal letters from Mr. Ernest J. Greenwalt, Refuge Manager of the Wichita Mountain Wildlife Refuge, and Mr. George E. Mushbach, Superintendent of Refuges, National Bison Range, Moiese, Montana. It appears that the bison herd of the National Bison Range (our samples coded BR) is derived from three distinct strains, the Conrad, the Goodnight, and the Corbin. Thirty-seven buffalo formed the original herd, which was established on October 16, 1909. These included thirty-four buffalo purchased by the American Bison Society from the Conrad estate at Kalispell, Montana; in addition the Conrad estate gave the Federal Government a bull and a cow. Charles Goodnight of Goodnight, Texas donated a pair of young buffalo but the male died before it could be transferred to the range. About a year later, three more buffalo were received from the Corbin herd. "The Conrad herd, from which most of the original stock for the range was obtained, originated in 1901 by the purchase of animals from the Pablo-Allard herd, which had been built up from a few calves captured about 1873 by Walking Coyote, a Pend d'Oreille Indian on the plains east of the main range of the Rocky Mountains." The herd on the Bison Range grew to number 640 in 1927; since that time it has been kept within manageable bounds by a yearly slaughter of excess animals.

The Wichita Refuge herd is derived from fifteen bison provided by the New York Zoological Park in 1907. It appears that these animals could represent four different strains, one from the Pablo-Allard herd, one from the Conrad herd and at least two other strains of unspecified origin. Since the establishment of this herd in 1907, six bulls have been introduced. Two of these were from the Davison ranch near Arnett, Oklahoma in 1928. These apparently made little contribution to the perpetuation of the herd. In 1942, four bulls were received from the Fort Niobrara Wild Life Refuge, Valentine, Nebraska. These were derived from a herd owned by J. W. Gilbert at Friend, Nebraska. By 1920, it had become apparent that restrictions would have to be placed on the size of the Wichita Refuge herd. At the time of this study the herd contained approximately 200 head—180 females and 20 males. A part of the surplus has been disposed of by sale or gift to zoos and other interested agencies in the United States and abroad.

The picture, then, is of two relatively small samples of populations reasonably well isolated from each other for a number of generations, but derived from somewhat similar foundation stock. This foundation stock represents a rather narrow basis of sampling from the original wild bison population. Furthermore, the populations have been maintained since early in the present century in relatively small numbers. Between the present-day bison and domestic cattle populations, and their common ancestors, a very long period is believed to have intervened.

Under these circumstances, it is remarkable that these bison populations are still segregating for a number of the cellular characteristics found in domestic cattle. The mechanism for the maintenance of this degree of similar heterogeneity must remain conjectural. Selection for heterozygosity at several of the loci would seem to provide the most likely single explanation.

Summary

Sixty-nine American bison and ten F_1 cattalo were typed with bovine blood-typing reagents.

None of twenty-one reagents known to react in the B system of bovine blood groups produced a reaction in bison blood typical of those encountered in the tests on the bloods of domestic breeds of cattle. This indicated that the B locus is either absent in bison or is occupied solely by alleles whose products, like that of the allele designated "*b*" in cattle, are essen-

tially non-reactive with the present battery of B system antibodies.

All of the bison bloods were lysed by the reagents X_1, X_2 and L′ of the C battery whereas individual differences were noted with the C system reagents C_1, C_2 and W. None of the bison bloods reacted with the R reagent of the C battery. The reactions with L′ were extremely weak and not typical of those encountered in the cattle tests whereas all bison bloods were strongly cross reactive with X_1 and X_2 reagents. The alleles C^{X_1}, C^{WX_1}, both of which are recognized in domestic cattle, and $C^{C_1WX_1}$ and $C^{C_2WX_1}$, neither of which has so far been encountered in domestic cattle, were indicated in bison. The possibility of the other C alleles, $C^{C_1X_1}$ and $C^{C_2X_1}$, could not be excluded.

Concerning the F-V locus of cattle, all sixty-nine bison appeared to be homozygous for an allele F^{V_2} not known in domestic cattle. The product of this allele, designated V_2, was differentiated by absorbing bovine anti-V with either bison blood or that of cattalo possessing V_2 in combination with F. The absorbed reagent, designated V_1, reacted with the bloods of V-positive cattle but not with bison bloods. The bloods of cattalo possessing phenogroup F inherited from domestic cattle and V_2 inherited from bison were hemolysed at approximately the same rate as bloods from individuals homozygous for F in tests with F dosage reagents.

The pairs of alleles *s* and S^S, *Z* and *z*, *a* and A^A, *J* and *j*, and *L* and *l* were indicated, respectively, at loci assumed to be equivalent or homologous to the S-U, Z, A-H, J and L loci of cattle. As in cattle, there was evidence of diversity in the *J* characteristics.

The blood factors H′ and Z′ were not encountered in testing these bison bloods. Assuming that the equivalent loci are present in bison, it seems probable that alleles *h′* and *z′* may be fixed at the respective bison loci.

Attempts to demonstrate a clearly definitive difference between the two species by means of cross-absorbing heteroimmune antisera prepared in both rabbits and cattle against bison and cattalo red cells were not successful.

The results were discussed in relation to the taxonomic status of the American buffalo as a species distinct from domestic cattle. Although no definite conclusions were reached, the differences between bison and domestic cattle appeared to be significantly greater than the between-breed differences encountered within domestic cattle. In spite of their long isolation from each other, domestic cattle and the bison have retained a surprising degree of similarity in their cellular antigens. The two herds of bison sampled show several significant differences from each other, which may be related to their somewhat different origins and the considerable period of isolation that has separated them.

Acknowledgment

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NOTES AND COMMENTS

THE CONCEPT OF ECOLOGIC NICHE, WITH REFERENCE TO THE THEORY OF NATURAL COEXISTENCE

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Ross (1957) in the pages of this journal has presented an interesting discussion of the natural coexistence of closely related species of leafhoppers in the same ecologic situation. The principle aim of his analysis was to demonstrate that Gause's Law was not a uniformly valid generalization. Gause's Law states that no two species have the same ecologic niche at the same time and place, or phrased differently, no two species have identical ecologies. Unfortunately, Ross' otherwise excellent account is marred by a fundamental confusion in the usage of the term ecologic niche which makes fallacious almost all of his conclusions.

Biologists in general have long been in basic agreement as to the meaning of the descriptive distributional terms range and habitat. Originally the two words had essentially similar connotations but they are now usually applied in different senses. The range of an organism is thought of as its broad geographic or physiographic occurrence. The range of the leafhopper *Erythroneura torella,* discussed by Ross, for example, might be stated to be: the central United States from Ohio, through Indiana to Illinois and eastern Kansas. Obviously few organisms have a continuous distribution throughout their range and almost always individuals of a particular form tend to occur only in scattered localities where favorable ecologic conditions exist. The general ecologic situations within the range where a species is found form its habitat. The habitat of *E. torella* according to Ross (p. 119), is sycamore trees in humid areas. The species is restricted to only a small portion of the total range of the host trees.

The term ecologic niche has in the past been utilized for two very divergent concepts. For many years numerous zoologists and almost all botanists have applied the term as meaning the same thing as habitat. The niche in this sense is equivalent to the biotope of Allee and Schmidt (1951: 165) or the habitat niche of Allee, Emerson, Park, Park and Schmidt (1949: 232). In recent years with the development of ecology as a science, ecologic niche has come to be utilized for a very different idea. Elton (1927: 63), Lack (1949), Odum (1953: 15), Andrewartha and Birch (1954: 3) and Clarke (1954: 468) all use the term in this newer sense. The ecologic niche of these authors does not refer to a place or environmental situation. Rather it is employed in a functional sense to describe the sum total of the activities of the organism. Particularly important to the understanding of the species niche are the organism's energy relations. What are its food sources? How does it fit into the general passage of energy through a particular food chain or web and through the ecosystem? But although this aspect is of fundamental importance, especially to animals, and is the feature stressed by most authors, it is only one of the total functional relations between organism and environment. Burrowing animals are excellent examples to illustrate this point. Not only do they have a definite predator-prey position in a given community but they modify the physical environment by their fossorial activities and provide shelter for other organisms in the tunnels they create. Any activity of an organism which modifies the substratum or medium of its environment by removal, addition or modification or affects other organisms through symbiotic or antibiotic factors constitutes a characteristic of the species' ecologic niche. For the sake of convenience it seems best to oriente the features of the niche around energy relations, but it must be remembered that prey-predator relations are not the only characteristics of an ecologic niche. Following this usage, *E. torella* would have a sycamore-leaf juice niche, in view of its feeding habits. However, this is only a partial description of the niche of this leafhopper and I cannot describe the animal's position in full since Ross does not present adequate data on the species' predators, parasites or other matters of utmost importance to the understanding of the functional place of *Torella* in its ecosystem.

Gause's Law (Lack, 1949; Odum, 1953) applies to the concept of ecologic niche in the functional sense. The essential feature of this generalization is the fact that no two species with identical niches (identical environmental relations) can occur together without one form being eliminated within a few generations through competition. Many forms may occur together in the same place or habitat, but within the habitat no two can have the same occupation or ecologic niche. Ross has attempted to repudiate this principle on the basis that several very closely related species of leafhoppers occur together in the same "ecologic niche." He con-

cludes that in many cases Gause's Law does not apply and calls situations where two forms occur in one "niche," natural coexistence. Unfortunately, Ross is not using the term ecologic niche in the connotation applicable to Gause's Law. He is instead utilizing the term as a synonym for habitat or place of occurrence. Thus all his comments regarding the "niches" of the several leafhopper species refer to their biotopes and not to their activities. Ross' critique of Gause's Law fails completely due to a misunderstanding of the dual usage of the term ecologic niche. Ross' conclusion that the related species of *Erythroneura* which occur together on Illinois sycamores and coexist in the same habitat must have similar ecologies is unquestioned. However, until he can present evidence demonstrating that these coexisting forms retain the same functional relations to the environment, provide identical predators and parasites with food and actually have wholly identical ecologies, he has no basis for the assumption that the several leafhopper species coexist in identical ecologic niches in the sense implied by Gause's Law.

In conclusion it must be pointed out that the functional concept of the ecologic niche is a most important idea to the understanding of modern community ecology and its use adds several dimensions to our concept of ecologic adaptation. It is unfortunate that its use is clouded by another frame of reference, particularly since the terms habitat and biotope are available for the concept of ecologic occurrence. For these reasons it is hoped that the term ecologic niche will gradually come to be used in both plant and animal ecology in a dynamic functional sense.

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FURTHER COMMENTS ON NICHES AND NATURAL COEXISTENCE

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I wish to thank Dr. Savage and Dr. Olson for allowing me this opportunity to reply to the aforegoing paper concerning the definition of *niche* and its application to the principles of natural coexistence.

Dr. Savage states that in five of the references he quotes, the ecologic niche is employed in a functional sense to describe the sum total of the activities of the organism, but in this assertion he is only partially correct. Of the five authors cited above by Savage, only Clarke (1954) gives a workable and unambiguous definition and description of an ecological niche: "Niche may be used in a broad sense to refer to the principal functions involved in the operation of the ecosystem, or it may be employed to describe the subdivisions of these and the various methods of 'making a living' within each functional category. Among herbivores that feed on trees, for example, some fill the niche of eating the leaves whereas others use the twigs, sap, bark, or roots as a source of food. In different geographical regions each type of niche is often filled by quite different species." As is readily seen, this treatment is based on the food-chain concept of community organization, the details of which may be expressed as the food activities of the organisms. Andrewartha and Birch (1954) mention *niche* only in passing. In their definitions both Elton (1927) and Odum (1953) associate at least three or four distinct ideas with the term *niche,* but it is interesting to note that when these two authors find use for the term, it is almost invariably in the food-chain concept expressed by Clarke. Lack (1949) uses niche in the same sense of a link in the food chain.

If *niche* is to be used for the purpose of aiding in the comparison of similar functions in different communities (and this is the avowed aim of Elton and Clarke), there seems no recourse but to use the term for a single function in the community structure. The ecologic relations of a species cannot be such a unit, because a single species may participate in many diverse functional spheres of community activity and different species which

coincide at one point of the community structure may not do so at others. The best solution seems to be the recognition of different types of niches (as Elton indeed does) but to give each a distinctive adjective, such as feeding niche, hibernating niche, nesting niche, and so on. In spirit this general idea was of course anticipated in other words by Allee, Emerson, Park, Park, and Schmidt (1949: 516). If one wishes a name for the items Dr. Savage wishes to include in the "species niche," there is one available—the term bionomics.

In this unitary (but still functional) manner niche refers to a point transfer of energy (as food or activity) within the community, a transfer which may be qualified as desired by the definer. Some animals have two kinds of food and therefore occupy two food niches, as explained by Elton concerning the Arctic fox and the hyena. Such dual-niche occupation is commonplace among insects, exemplified by the many species of mosquitoes whose larvae occupy the herbivore niche and whose adults occupy the vertebrate-blood-feeding niche.

The predators which feed on a species are not part of the latter's niche. These predators represent a second niche relationship at another level of community organization. This point also is recognized specifically by Elton: "One of the biggest niches is that occupied by small sap-suckers, of which one of the biggest groups is that of the plant-lice or aphids. The animals preying upon aphids form a rather distinct niche also. Of these the most important are the coccinellid beetles known as ladybirds, together with the larvae of syrphid flies and of lacewings." Dr. Savage's insistence that the predators of the six species of *Erythroneura* leafhoppers must be identical in order that these leafhoppers have the same ecological niche is therefore not relevant.

The six species of *Erythroneura* referred to in my paper on natural coexistence all live in exactly the same habitats—duff in winter, anything green in spring, sycamore leaves during the entire breeding season. They not only feed on the same leaves but both mixed and single species colonies produce exactly the same pattern of leaf-feeding punctures, indicating that they suck juices from comparable cells and thus alter the environment in the same way. The seasonal history of all six species is identical in the same location hence comparable life history stages are feeding at the same times. It is thus clear that they all occupy the same set of niches. It may be of interest to note here that our knowledge of leafhopper predators as a whole suggests that all six species of leafhoppers mentioned here have identical species of predators.

Dr. Savage further states that I do not use niche in the same sense as did Gause. Gause (1934) indubitably implies that in his experiments with competitive herbivores (not his prey-predator studies) he considers each species of *plant* as one of the "major niches" of his artificial microcosm, and that several species of Protozoa (having different ecologies!) may potentially occupy each of these food niches. Gause simply asserts that no two species *can occupy* the same niche at the same time and place. This contention does not allow the rephrasing made by Dr. Savage. Certainly there is no conflict here between the niche concept employed by Gause and that used by me in discussing the sycamore leafhopper situation.

Contrary to Dr. Savage's statements, the definition of niche is only incidental to the main point put forward in my report on the sycamore leafhoppers. In whatever fashion the niche is defined, the fact remains that, in that large proportion of the group's range where all occur together, the six species of leafhoppers feed on the same part of the same plant at the same time and in the same way during the entire productive parts of their life cycles. This is the most direct kind of potential competition and affords an example in nature of the kind of competitive relation that Gause was studying in cultures. It is primarily with this competitive facet that my paper deals.

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THE COMPARISON OF OBSERVED AND CALCULATED ZYGOTIC DISTRIBUTIONS

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In a recent article (1957) Epling, Mitchell, and Mattoni state that in view of the strong selection that takes place during the seasonal fluctuations of inversion frequencies in *Drosophila pseudoobscura,* it is surprising to find no indication of it in the differential survival of

zygotic combinations. They suggest that selection may be operating on other attributes that do not affect the Hardy-Weinberg ratios. I would like to make a somewhat different suggestion; namely, that the calculation of expected zygotic frequencies by the application of the binomial expansion to observed gametic frequencies and the genotype-by-genotype comparison of observed and expected zygotic frequencies can lead to serious errors. This was the essence of a personal letter to White to which he has referred (1956, footnote p. 307).

The type of calculation to which I refer is a common one in population genetics. The relative frequencies of individuals of different genotypes (zygotic frequencies) are determined by sampling a population. From the observed zygotic frequencies, gametic frequencies are determined; in the case of three contrasting genotypes—*AA, Aa,* and *aa*—gametic frequencies are easily computed by adding one half of the frequency of heterozygotes to each type of homozygote. These observed gametic frequencies are then used to calculate zygotic frequencies expected on the basis of the binomial expansion—p^2 *AA*, $2pq$ *Aa*, and q^2 *aa* where p and q are the observed frequencies of *A* and *a*. The observed and expected distributions can be compared (for instance by chi-square with one degree of freedom in the above example) in order to determine whether they differ significantly. A number of workers, Levene and Dobzhansky (1948) and Hexter (1955) as well as Epling and White have used significant deviations as a basis for comparing the relative adaptive values of the different genotypes. The comparison of zygotic distributions is a legitimate procedure under any circumstances. The comparison of observed and expected frequencies of individual genotypes between these distributions assumes that gametic frequencies have remained constant from the beginning of the generation sampled.

A much more elaborate discussion of the problem than that which follows will be presented by Novitski and Dempster in a forthcoming issue of Genetics; the following examples are given here to acquaint readers of EVOLUTION with some of the pitfalls which accompany the misapplication of the Hardy-Weinberg equilibrium and to draw their attention to the more extended analyses of Novitski and Dempster. For our purposes it is sufficient to use a particular numerical example: Assume that within a population the genes *A* and *a* have frequencies of 70% and 30%, respectively. Assume, too, that mating is at random so that the initial zygotic frequencies of a given generation are *AA*–49%; *Aa*–42%; and *aa*–9%. Let's now calculate the final zygotic frequencies, final gene frequencies, expected zygotic frequencies, and apparent adaptive values under two conditions. Case 1: *AA, Aa,* and *aa* have real adaptive values of 1.0, 0.6, and 0.2, respectively. Case 2: *AA, Aa,* and *aa* have real adaptive values of 0.2, 0.6, and 1.0, respectively. It is obvious that in the first case gene *a* is rare and becomes rarer, while in the second it increases in frequency. It is also obvious that sizable selective forces are postulated in this population. The calculations are indicated in the following table:

	Gametic frequencies		Zygotic frequencies			
	A	a	AA	Aa	aa	Total
Case 1:						
Initial	70	30	49	42	9	(100%)
Adaptive value	—	—	1	.6	.2	
Final	—	—	49	25.2	1.8	(76.0%)
Observed	81.1	19.0	64.5	33.2	2.4	(100%)
Expected	—	—	65.8	30.8	3.6	(100%)
Obs./Exp. (Hetero = 1.00), or Apparent adaptive value	—	—	.91	1.00	.62	
Case 2:						
Initial	70	30	49	42	9	(100%)
Adaptive value	—	—	.2	.6	1	
Final	—	—	9.8	25.2	9.0	(44.0%)
Observed	50.9	49.1	22.3	57.3	20.5	(100%)
Expected	—	—	25.9	50.0	24.1	(100%)
Obs./Exp. (Hetero = 1.00), or Apparent adaptive value	—	—	.75	1.00	.74	

Recalling that the observed zygotic frequencies totaling 100% represent the first available information concerning the population in either case, one can see from the table that no hint of the enormous selective differences between zygotes of different genotypes is obtained by comparing observed and expected zygotic frequencies. An analysis of 500 individuals would probably fail to indicate a significant difference between the observed and expected zygotic distributions in the first case. A comparison of the observed and expected frequencies of individual genotypes between these distributions would lead to the following errors: (1) A woefully inadequate estimation of the intensity of selection. (2) An apparent superiority of heterozygotes where there is actually strong selection against these individuals. (3) In case 2, an apparent selective superiority of the poorer over the better of the two types of homozygotes which are, in fact, the individuals favored by selection within this population.

Excepting the trivial cases in which the frequency of *A* equals either 100% or 0%, the initial zygotic frequencies of *AA, Aa,* and *aa* individuals *whatever they may be* can be transformed into virtually any other set of frequencies by selection; the limitation in this respect is imposed solely by the initial numbers of zygotes and by the proportion of mortality during development. Consequently it is impossible to use final zygotic and gene frequencies of a single sample to predict the course selection has taken in giving rise to these frequencies; other information leading to a reliable estimate of initial gametic or zygotic frequencies is essential.

I would like to acknowledge the discussions I have had on this problem with Howard Levene and Edward Novitski.

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HAPLODIPLOIDY IN THE DIASPIDIDAE—CONFIRMATION OF AN EVOLUTIONARY HYPOTHESIS

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In 1931, Schrader and Hughes-Schrader advanced an hypothesis to account for the evolution of male haploidy in the superfamily comprising the coccids (Coccoidea). They proposed that the *type* of chromosome behavior observed in the section Lecanoidae (classification of Balachowsky, 1942) had closely preceded the establishment of male haploidy in the tribe, Iceryini, of the section Margaroidae, although these two groups obviously stood in no such phylogenetic relationship to each other.

In the lecanoids, one haploid set becomes heterochromatic during early embryogeny of the males and is eliminated during spermatogenesis. As far as chromosome number is concerned, the males are diploid although they breed as haploids; if the heterochromatic set is genetically inert, they are virtual haploids. According to Schrader and Hughes-Schrader, the degeneration or inactivation of the heterochromatic set may lead eventually to its complete elimination. On acquisition of the ability of eggs to develop without fertilization, true male haploidy would thus be established through a series of gradual transitions.

Both the lecanoid system just described and the margaroid haplodiploidy seem to be derived from more primitive members of each group which have XX-XO sex determining mechanisms. It is clear on this, as well as other grounds, that the margaroid haplodiploidy was not derived directly from the lecanoid system. However, the lecanoid system may well illustrate "the type of changes capable of establishment in coccid chromosome cycles—some or all of which may have been instrumental in or incidental to the establishment of haploidy in the Iceryini" (Hughes-Schrader, 1948).

The third section of the coccids, the Diaspidoidae, consists of two families (sometimes subfamilies), the smaller Phoenicococcidae, and the larger, economically important Diaspididae. This section consists of highly specialized forms and is undoubtedly derived from ancestral types of lecanoid affinities. In fact, one small family, the Conchaspidae has recently been associated

with both the lecanoids (Balachowsky, 1942) and the diaspidoids (the ramus Diaspidi, Ferris, 1957). (Ferris divides the Lecanoidae into four rami in rank equal to the Margarodi and Diaspidi; of these, two possess the lecanoid chromosomal system, the Eriococci and the Cocci, while the other two, Lacciferi and Beesonii, have yet to be studied cytologically.)

Recent cytological studies (Lindner, 1954; Brown and Bennett, 1957; Brown, unpublished) indicate that many of the Diaspididae are true haplodiploids. Of the fifteen bisexual species so far studied, twelve are haplodiploid. The other three show a lecanoid-like system in that one chromosome set becomes heterochromatic in early embryogeny; however, details of spermatogenesis, which is not typically lecanoid, are known for only one of these species, *Comstockiella sabalis* (Comstk.) (Brown, 1957), a morphologically atypical member of the family. Preliminary observations on one member of the Phoenicococcidae, *Phoenicococcus marlatti* Ckll. (Brown, unpublished) reveal heterochromatization of one haploid set in some of the embryos; again, a lecanoid or lecanoid-like system.

The haploid males of the Diaspididae become so through elimination of the paternal chromosome set during early embryogeny (Brown & Bennett, 1957; Brown, unpublished), near the time at which heterochromatization begins in the lecanoid or lecanoid-like systems. Thus, the achievement of haploidy is not through the bypassing of fertilization but by a process developmentally related to the heterochromatization of one haploid set.

The recent cytological findings confirm the Schraders' hypothesis that the lecanoid system of chromosomal behavior can provide the basis or the "raw material" for the evolution of haplodiploidy in the coccids. In so far as the coccids are concerned, they would apparently answer the objection of Whiting (1945) that heteropycnosis and male haploidy are independent phenomena. White (1954, p. 238) also does not seem to subscribe to the idea that heteropycnosis of one chromosome set in the lecanoid males leads to virtual haploidy: "At present all that one can safely conclude is that the [lecanoids] have lost the original XO : XX sex-determining mechanism . . . and acquired some new type of mechanism which apparently cannot be demonstrated by direct cytological means." Although the Schraders' hypothesis has been confirmed, the author is sure that all those concerned with the problem will agree that further clarification will depend on appropriate testing of the lecanoid genetic mechanism (Hughes-Schrader, 1948).

Another part of the Schraders' hypothesis seeks to explain an earlier phase in the evolution of the lecanoid system and deals with asynchrony and asynapsis of one chromosome set as preliminary or conjunct processes in the development of heteropycnosis. No further evidence in this matter has appeared since the review of Hughes-Schrader (1948) on the cytology of the coccids.

The coccids have long been noted for their unusual systems of chromosome behavior. It is also noteworthy that, when precisely studied, such systems can be shown to be related to each other in such a logical fashion that prediction is possible.

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THE CAUDAL FIN AS A HYDROFOIL

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The stimulating paper by Savile (1957) dealing with the aerodynamic specializations of the avian wing has brought to mind rather similar comparisons made between types of caudal fins of fish. The caudal fins of fish act as foil structures to provide a substantial part of the thrust used in propulsion. Looked upon as a hydrofoil, a tail fin can be described in hydrodynamic

(or aerodynamic) terms. This description can often be shown to have biological significance.

Interesting results are obtained if one compares the aspect ratios of the caudal fins of different species of fish. Aspect ratio (AR) is defined as the span of the foil/chord; this is often more conveniently stated as span^2/area. As a general rule, aerodynamic efficiency improves as the aspect ratio increases, to about AR values of 8 to 10. Beyond this, efficiency is sharply reduced as bulky structural members are required to support the wide span.

The following are some measurements of AR in fish:

Bowfin (*Amia calva*)	1.0 (fin extended)
Lake trout (*Salvelinus namaycush*)	1.0 (fin relaxed)
Lake trout	2.0–2.5 (fin extended)
Smallmouth bass (*Micropterus dolomieu*)	2.0 (fin extended)
Striped pargo (*Hoplopagrus guntheri*)	1.5 (fin relaxed)
Striped pargo	2.9 (fin extended)
Yellow perch (*Perca flavescens*)	3.2–3.8 (fin extended)
Green jack (*Caranx caballus*)	3.8
Sierra mackerel (*Scomberomorus sierra*)	4.1
Black skipjack (*Euthynnus lineatus*)	5.0
Little tuna (*Euthynnus alletteratus*)	5.0
Yellowfin tuna (*Neothunnus macropterus*)	5.2
White marlin (*Makaira albida*)	6.1

The last six fish in the list have rigid caudal fins which are permanently extended.

The list shows *Amia* to have an AR = 1. It is generally accepted that the Holostei are the precursors of the Teleostei, from which it might be inferred that the low AR of the caudal fin of *Amia* (and *Lepidosteus*) is primitive. It is doubtful that this inference is justified. Probably some sort of heterocercy was a primitive feature of actively swimming early fish. From a heterocercal tail fin it is as easy to derive a forked tail of from moderate to high AR as it is to derive a rounded tail of low AR. Many holosteans, including some believed to lie on the ancestral line of the bony fish, had, in fact, forked tails, obviously of high AR (e.g., illustrations in Rayner, 1941). The same thing can be seen in groups even more primitive than the Holostei. The presence of a fin of high AR means only that its possessor was, or is, specialized for speedy swimming. So, except within comparatively small, well-defined groups of fish, the shape of the caudal fin cannot be used in phylogenetic speculation. The shape of the fin may be used, however, to aid in drawing conclusions about the mode of life of a (fossil) fish. Or, on the other hand, appreciation of the relationship between speed and the form of the caudal fin may be of assistance in the restoration of fossil forms for which the postanal skeleton is lacking. I have in mind specifically the reconstruction of *Dinichthys* by Heintz (1932) in which a macruriform body was proposed to propel that fearsome head. I would hold out for some sort of forked fin.

There is a large group of fish which may be called "typical" in their appearance and swimming behavior, although they do not form a natural taxonomic assemblage. They are represented in the list above by the trout, the bass, the pargo and the perch. Each has a flexible caudal fin that can be moved ray by ray in various ways by a rather complex intrinsic musculature derived from the lateral musculature. The intrinsic caudal musculature is remarkably similar throughout a wide variety of fish. These fish can hover nearly motionless in the water or they can dart forward with considerable speed. For all species in the "typical" group the caudal fin provides approximately the same amount of locomotor thrust. To compare this with the wings of birds, the tail fin thrust is equivalent to wing lift. The "typical" fish are provided with a fin AR of low to intermediate efficiency in aero- or hydrodynamic terms. High AR does not improve the efficiency of a flexible tail fin. Probably a fantail goldfish can be shown to have a caudal fin of tremendous AR, but it does the fish little good, for the long tapering ends contribute drag instead of thrust. Undoubtedly, among the fish concerned, the flexibility of the caudal fin fully compensates for the small AR. In what manner the flexibility of the fin affects its hydrodynamic characteristics is yet undetermined. Perhaps the flexibility of the tail fin adds to the stability of the hovering or cruising fish. Unlike the wings of some birds, the caudal fins of fish are not slotted to increase lift (thrust) characteristics; perhaps at high speed the flexible fin spills water to prevent loss of power in turbulence. Almost undoubtedly the forked fin with pointed tips helps reduce turbulence. Note also Gray's Paradox (Gray, 1936; 1957; Parry, 1949); does the flexible fin contribute to the postulated maintenance of laminar flow along the body of the swiftly swimming animal?

The difficulties in attributing standard quali-

ties to characteristics such as AR of a flexible fin are illustrated in the list above. Because a fish can relax or extend a flexible fin voluntarily, the AR of that fin can be rapidly changed. Presumably the hydrodynamic characteristics of the fin will be changed at the same time. It is the functions of the changing characteristics that we do not understand. In the list above it is a single lake trout whose tail fin AR varied from 1.0 to 2.0 as the fin was extended. A different individual had a measurement of 2.5 for the extended fin. The pargo listed twice above was the same individual. A further difficulty arises when we cannot define exactly the maximum extended size or the minimum relaxed size of the fin which the fish can normally achieve. For the measurements recorded here, extension was taken as the fullest spread of the fin that could be made without tearing the membranes; relaxation was taken as the position in which the fin was found after fixation of the specimen.

It is among the rapid swimmers, jacks and tunas, that AR becomes particularly important. The AR is relatively large and the caudal fin is rigid. Specializations towards ability to swim rapidly show as morphological changes and differences in the manner of swimming. For instance, the rigid caudal fin of the speedy tuna does not require the intrinsic musculature present to control individual fin rays in soft-finned fish. The wave characteristic controlling thrust becomes frequency, not amplitude. The vertebral column is relatively inflexible, with perhaps something of an elastic return (Rockwell, Evans and Pheasant, 1938). The lateral musculature is concentrated further craniad than that of the "typical" fish. The caudal peduncle is very slim. The peduncle and the base of the fin are inhabited chiefly by tendons running back from the lateral musculature and by vestiges of the intrinsic caudal muscles, which remain as fibre groups and delicate tendon slips.

As the improvement in plan design of an aerofoil has followed internal structural support, so in the jacks and tunas the caudal skeleton has been improved to allow a significant increase in AR. Not only have the fin rays been stiffened and flattened to form a solid skeletal sheet, but the bases on which these rest, the urostyle and epural and hypural plates, have been modified too. The commonly found heterocercy of the teleost caudal skeleton has been greatly reduced. The tail skeleton has become, for all practical purposes, dorsoventrally symmetrical. Only the vestigial muscular soft parts show clearly the antecedent heterocercy.

The greatest AR I have measured is 6.1, obtained for a white marlin. This would appear to be close to the upper limit. The fin rays of the marlin are bony, but they tend to become flexible at their tips because the span is so great and the fin is so thin in section. To increase the span much would require either a loss of rigidity of the fin or a marked increase in its thickness. A thickening of the fin would shift the centre of buoyancy of the fish and change the foil characteristics of the fin. Undoubtedly some sort of modification of the lateral musculature would follow. The result would be an altogether different type of fish. This is not impossible; it just does not seem to have happened among fish.

Differences in swimming ability are probably indicated by the differences in AR shown between the green jack, the mackerel, the skipjack and the yellowfin tuna. It appears to me to be safe to assume that the efficiency of a rigid fin will be closely related to the fin's foil characteristics, of which AR is probably the most important. If this is the case, the tuna is a better swimmer than the skipjack, the skipjack a better swimmer than the mackerel, and the mackerel better than the jack. The differences between mackerel and skipjack or tuna also probably indicate phylogenetic improvement within a group, the mackerel being a less specialized scombroid than the other two. However, the exact relationship of skipjack to tuna is open to debate and the nature of the caudal fin, by itself, does not seem to contribute much.

Questions concerning the correlation of swimming ability to fin form could be answered with complete confidence were there a body of information dealing with the speeds of fish, particularly maximum and cruising speeds and rates of acceleration, together with measurements of length and weight of the specimens studied.

The scombroid fish (mackerels and tunas, etc.) show an interesting specialization with the development of finlets along the dorsal and ventral midlines of the caudal peduncle. These finlets probably function as slots which, although not part of a foil, serve to increase the thrust provided by the tail and to decrease the turbulence produced by the lateral oscillation of the peduncle in swimming. This is rather different from the flow separation suggested by G. E. Gadd (Gray, 1949). Each finlet is provided with a discrete musculature of its own; therefore it seems likely that considerable control can be exercised over the functioning of the finlets. I suggest that the finlets flap back and forth as the peduncle oscillates from side to side. Contraction of the finlet muscles limits the freedom of movement of the finlets. The muscles do not actively move the finlets but the resistance of the muscles to the pressure of the water controls the angle of the finlets, which controls the aperture of the slot between neighbouring finlets. It should be noted in passing that the caudal extensions of the dorsal

and anal fins of jacks (Carangidae) have serrated edges which may provide simple and relatively inefficient peduncular slots for these fish (cf. primitive V slots of Savile, *op. cit.*).

The fleshy, lateral peduncular keel of scombroids obviously streamlines the oscillating peduncle, perhaps to reduce the incidence of vortex streets, as suggested by Harris (1950). However, I believe that two other functions of the keel may be more important. The keel is composed of dense connective tissue, and in some species it has a skeleton of modified scales. The keel forms a terminal connection for some of the superficial tendons leading to the tail from the lateral musculature. The keels serve as spreaders or lever arms for the tendons to increase the mechanical advantage of the muscle. The keel may also serve to direct the flow of water passing back to the tail fin. A directing function would serve to damp dorso-ventral turbulence in the stream flow, serving to keep laminar the flow over the caudal fin. Certainly the paired lateral keels on each side of the marlin fin do not laterally streamline the peduncle. Although the marlin is not a scrombroid, the peduncular keels serve a homologous purpose. Presumably the keels of jacks, certain sharks and cetaceans and others have also a similar function.

While the scombroids have evolved to swiftly swimming forms, two types of swimmers exemplify other evolutionary trends among the fish. One type comprises the eel-like fish whose bodies provide a greater share of the thrust. Here an indeterminate, but large, area of definite span provides thrust, hence AR is a very small quantity. Eels develop thrust by means of body waves of large amplitude and relatively slow frequency. The converse is true for tuna, as observed above. However, swimming is still basically the same, performed by lateral undulations of the body.

The plectognath fish (puffers and trunkfish, etc.) vary the theme in yet another way. Slow and inefficient swimmers when compared to the wide-ranging pelagic species, plectognaths possess a small caudal fin that suffices only to scull them through the water in the manner described by Breder (1926). The more specialized members of this group, e.g., *Mola, Ranzania,* supplant caudal fin function by the use of dorsal and anal fins. They lose the lateral musculature which is the source of locomotor power for all but a few other fish, e.g., the seahorse, *Hippocampus.* The molid style of swimming is entirely different from that of all other types of fish (Raven, 1939a; 1939b; Amadon, 1943).

We can see, then, that swimming ability, tail form and musculo-skeletal changes vary together along the different paths of evolutionary deployment of fish. These are the characteristics that are found in combination:

1. A fish (e.g., eel) that swims with large amplitude and relatively low frequency undulations of the body has:

a) a very flexible vertebral column of many short vertebrae;
b) a thick, muscular body and caudal peduncle;
c) a rounded tail fin with a negligible AR.

2. A 'typical' fish (e.g., perch) which combines moderate amplitude and fairly high frequency to form swimming waves has:

a) a flexible vertebral column of short vertebrae, the number of which may range from 24 to a few more than 100, but commonly numbers from 35 to 70;
b) a definitely narrowed but muscular caudal peduncle;
c) a flexible, forked tail fin of intermediate (2 to 4) AR.

3. A fish that utilises a wave of low amplitude but very high frequency (e.g., tuna) has:

a) a stiff, perhaps elastic, vertebral column of long vertebrae, commonly numbering from 30 to 45, and with well-developed zygapophyses;
b) a slim, essentially non-muscular peduncle;
c) a rigid tail fin of high AR (5 to 6).

4. The slow, awkward plectognaths have:

a) a remarkably short vertebral column of from 14 to 20 vertebrae which has limited flexibility;
b) a lateral musculature which is poorly developed or is entirely lacking;
c) a flexible tail fin of low or negligible AR (note that for molids AR calculations should be made on dorsal and anal fins rather than the caudal).

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REPORT ON THE TWELFTH ANNUAL MEETING OF THE SOCIETY FOR THE STUDY OF EVOLUTION, AUGUST 26, 1957

HARLAN LEWIS

The Twelfth Annual Meeting of the Society was held at Stanford University, August 26–29, 1957, under the sponsorship of the A.I.B.S.

At the business meeting, the time and place of the next two annual meetings was announced. In 1958, the meeting will be held at the University of Michigan, Ann Arbor, August 31–September 3. Warren H. Wagner, Jr. is chairman of the local committee. This meeting will begin three days after the close of the X International Congress of Genetics at Montreal and two days after the A.I.B.S. meetings at Indiana University. The annual meeting in 1959 will be held at the University of Chicago in November in conjunction with their Darwin Centennial Celebration which the Society is sponsoring. Everett C. Olson is chairman of the local committee.

The Secretary announced that a new membership list has been prepared showing a membership of 898. Since publication of the last list three years ago, we have gained 222 new members but have lost 216 through death and resignations leaving a net gain of only 6. Of the 676 "old members" listed in the new directory, 200 have changed their address at least once during the last three years. The 236 most recent members include 146 that are primarily interested in a living group of animals, other than man, or use animals as research material; 47 are primarily interested in plants or work with them; 18 are paleontologists; 2 are anthropologists; and 23 are interested in general biology or miscellaneous fields such as the history of biology. Among those zoologically inclined, 68 are primarily interested in a particular group of animals or a fauna; 42 are primarily interested in genetics or hybridization; 20 in ecology or behavior; 16 in evolutionary mechanisms. The botanists indicated comparable interests in about the same relative frequencies: systematics 21, genetics 18, ecology 6, evolutionary mechanisms 2.

The Secretary also reported on the action taken by the Council at its meeting, including a decision to discontinue an arrangement made in 1946 with the British Association for the Study of Systematics in Relation to Biology whereby their members could receive EVOLUTION for $4, without membership in the Society for the Study of Evolution.

The Treasurer presented a report for 1956 showing that receipts exceeded expenditures by $100.25. An interim report on the current financial status of the Society indicated that because of increased publication costs we will probably have a deficit this year. No increase in dues was recommended for the present, but unless there is an increase in membership or subscriptions, an increase in dues may have to be considered next year.

The Editor's report indicated that the rate of receipt of manuscripts increased rapidly during the last six months, to the extent that it has been necessary to increase issue size for June and September of 1957 to accommodate good manuscripts and maintain a reasonable interval between date of receipt and publication. The present interval is about 8 months but will decrease somewhat with the next two issues. Foreign manuscripts continue to make up about 40 per cent of the titles received and reports from Associate Editors traveling abroad indicate a widespread interest in EVOLUTION and an appreciation of its cosmopolitan character. The majority of papers received report results of specific researches, with purely theoretical studies represented primarily in short notes. Very few manuscripts directed toward syntheses beyond narrow fields have been received. Since EVOLUTION is particularly suited to broad papers, the Editor wishes to encourage authors to submit such papers.

President Muller pointed out the need for funds to provide travel grants to overseas geneticists attending the X International Congress of Genetics in Montreal, a Congress of which the Society for the Study of Evolution is a sponsor. On recommendation of the Coun-

cil he suggested that the members of the Society residing in the dollar area be requested to make a voluntary contribution of $2 or more to this fund, the contribution to be collected with the dues for 1958. James Walters put this suggestion in the form of a motion that carried by unanimous vote.

The symposium "Evolutionary Aspects of Human Behavior" arranged by President Muller and cosponsored by the Genetics Society of America, was a feature attraction of the meetings and was held midst the splendor of the new Dinkelspiel Auditorium. Curt Stern presided. The papers presented were: "Behavioral Factors in Human Origins" by S. L. Washburn, "Structure in Generalized Hunting and Collecting Populations," by J. B. Birdsell, "Psychological Evolution and Human Behavior," by L. Z. Freeman and Anne Roe, "The Problem of the Evolution of Culture," by Julian H. Steward (read by Curt Stern), and "Human Values in Relation to Evolution," by H. J. Muller.

The Society also sponsored a very successful symposium "The Origins and Affinities of the Land and Freshwater Fauna of Western North America" arranged by the Pacific Section of the Society of Systematic Zoology.

The following contributed papers were presented:

ABPLANALP, H., U. K. ABBOTT, and V. S. ASMUNDSON, University of California, Davis. Evolutionary significance of interruptions in development of avian embryos of diverse origins.

ASMUNDSON, V. S., and F. X. OGASAWARA, University of California, Davis. Segregation among backcross progeny from a turkey species cross. (*Meleagris ocellata* × *M. gallopavo*).

BENNETT, JOHN, Stanford University. The rise of biological organization and the problem of higher categories.

BLAIR, W. FRANK, University of Texas. Mating call in the speciation of anuran amphibians.

DALY, KEVIN, Cornell University. Biometrical analysis of interspecific differences in the genus *Nicotiana*.

DOWN, THEODORE, Los Angeles County Museum. Microevolution in *Merychippus* from the Miocene of Western North America.

GHENT, ARTHUR W., and D. R. WALLACE, Forest Insect Laboratory, Sault Ste. Marie, Ont., Canada. Ecological speciation in certain *Neodiprion* sawflies, as indicated by their oviposition behavior.

GERSTEL, D. U., and L. L. PHILLIPS, North Carolina State College. Genetic segregation in amphiploids synthesized from tetraploid cotton and diploid relatives.

GRUN, PAUL, and DOLORES MCHUGH, Pennsylvania State University. Isolating barriers operating between diploid species of *Solanum*.

HAPP, GEORGE B., Principia College, Elsah, Ill. Evolution and ecological sequences.

HEYNEMAN, DONALD, University of California, Los Angeles. On the origin of the digenetic trematode life cycle.

HILDEBRAND, MILTON, University of California, Davis. Cosmic events and perspective in organic evolution.

HUBBS, CLARK, University of Texas. Population analysis in a hybrid swarm of *Gambusia* (Osteichthys).

JAMESON, DAVID L., University of Oregon. Altitudinal races of the Pacific Tree-Frog, *Hyla regilla*.

LEE, JOSHUA A., University of California, Davis. Investigations into the nature of intervarietal competition in barley.

MALOGOLOWKIN, CHANA, Centro de Pesquisas Geneticas, Rio de Janeiro, Brazil. Cytoplasmically inherited sex-ratio conditions in *Drosophila*.

MICHENER, C. D., University of Kansas. Evolution of social behavior among halictine bees.

MYERS, GEORGE S., Stanford University. Some trends in the evolution of teleostean fishes.

RICK, CHARLES M., University of California, Davis. Developmental and genetic aspects of barriers to interbreeding between subspecies of *Lycopersicon peruvianum*.

ROSS, HERBERT H., Illinois Natural History Survey. Evidence of the hybrid origin of certain leafhopper species.

SAVAGE, JAY M., and ARDEN H. BRAME, JR., University of Southern California. The Southern California slender salamanders: a solution of the *Batrachoseps* problem.

SMITH, BEN W., North Carolina State College. Chromosome behavior and sex-expression in hybrids between dioecious *Rumex* species which differ in chromosome number.

SMITH, STANLEY G., Forest Insect Laboratory, Sault Ste. Marie, Ont. Adaptive chromosomal evolution in *Chilocorus stigma*.

STEBBINS, G. LEDYARD, University of California, Davis. Relic genes in an autotetraploid subspecies of *Dactylis*.

STEFFENSEN, DALE, Brookhaven National Laboratory. Changes in Selective patterns as influenced by metal ion nutrition of *Drosophila melanogaster*.

TUCKER, JOHN M., University of California, Davis, *Quercus undulata:* An unusual hybrid complex in the southern Rocky Mountain region.

VICKERY, ROBERT K., JR., and BARID B. MUKHERJEE, University of Utah. Evolution by aneuploidy and polyploidy in the *Mimulus guttatus* complex.

WHITE, M. J. D., University of Missouri. Cytotaxonomy of a group of Australian grasshoppers.

WILLIAMS, GEORGE C., Michigan State University. Natural selection of parental care in fishes.